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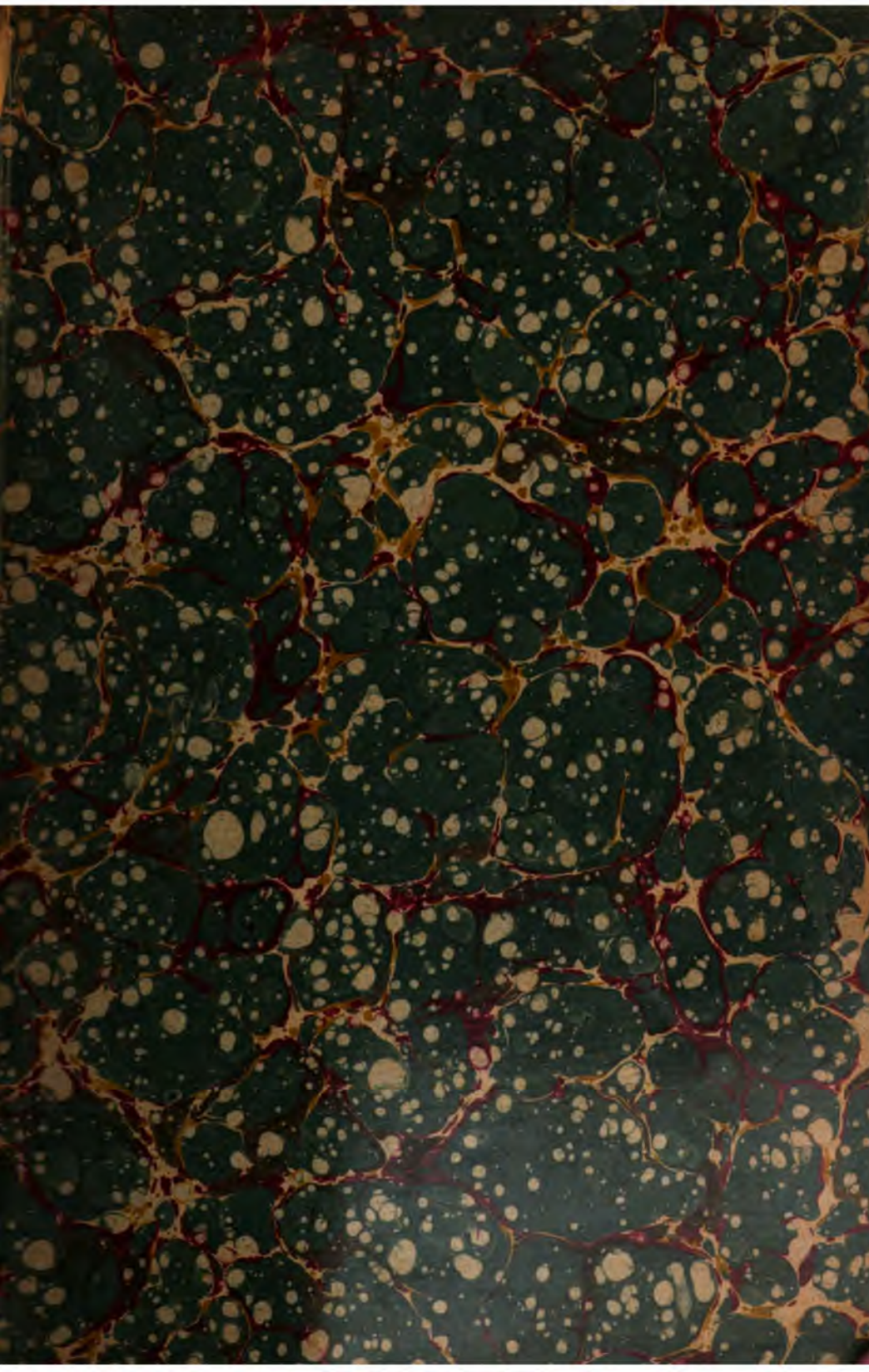
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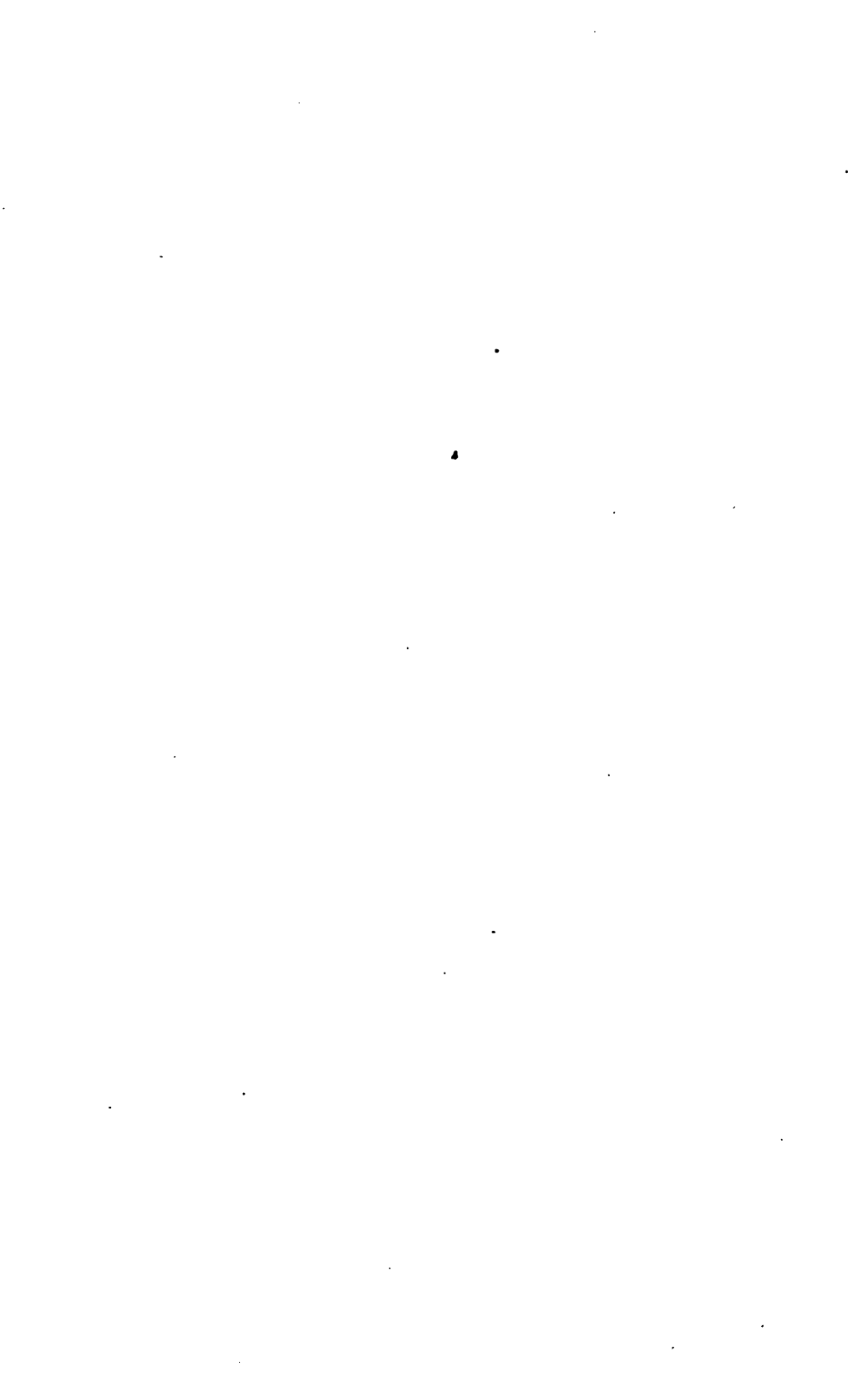
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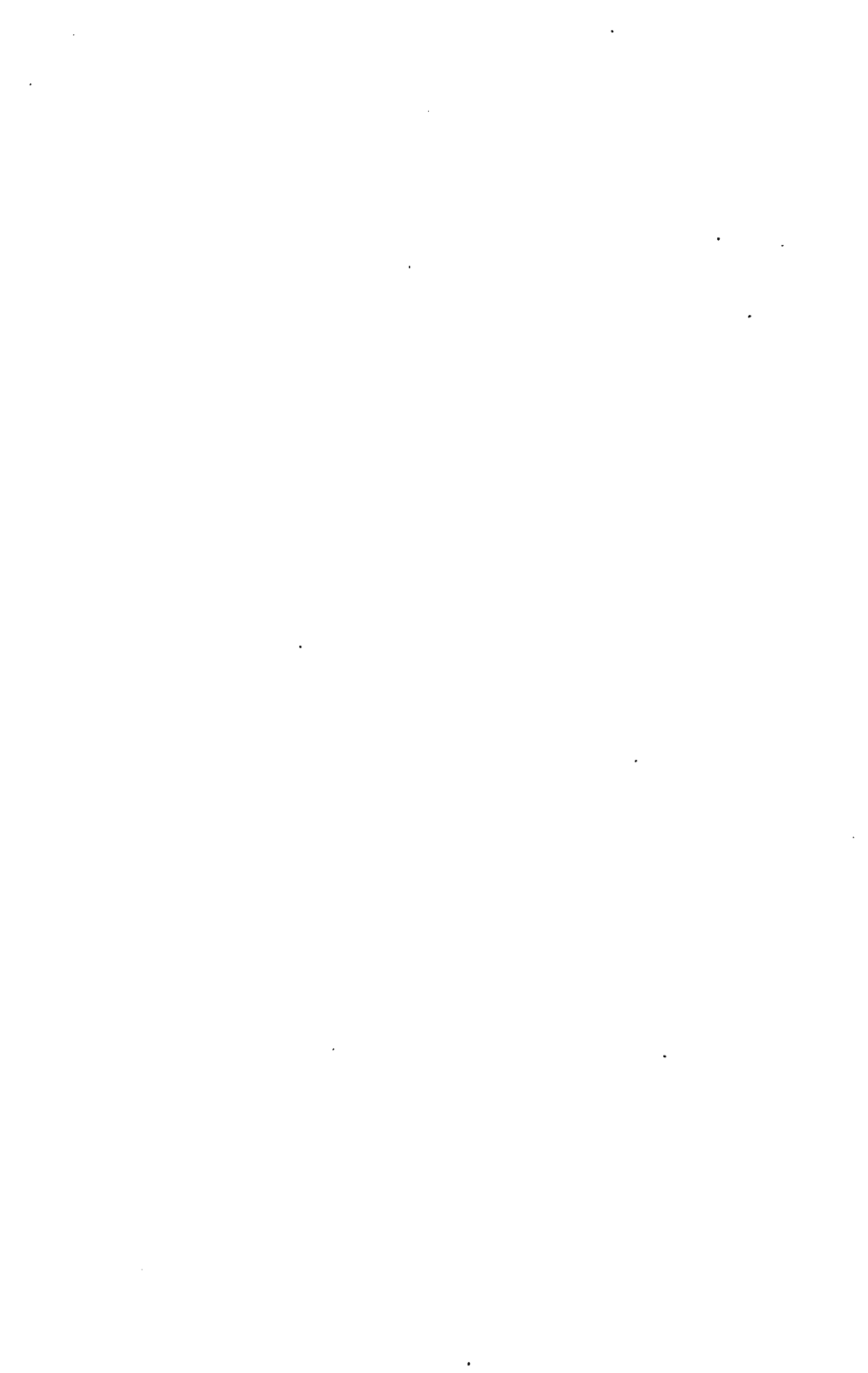












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PROCEEDINGS  
OF THE  
AMERICAN PHILOSOPHICAL SOCIETY  
HELD AT PHILADELPHIA FOR PROMOTING USEFUL KNOWLEDGE.

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It is requested that all correspondence be addressed

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*Stated Meeting, January 3, 1902.*

Curator LYMAN in the Chair.

Present, 6 members.

Prof. Dana C. Munro, a newly elected member, was presented to the Chair, and took his seat in the Society.

The list of donations to the Library was laid on the table and thanks were ordered for them.

The decease of Mr. Clarence King, at Phoenix, Ariz., on December 24, 1901, aged 60 years, was announced.

Prof. A. Radcliffe Grote presented a paper entitled "Results Obtained from a Search for the Type of *Noctua* Linn., and Conclusions as to Types of Hubnerian Noctuid Genera Represented in the North American Fauna."

Prof. J. Dyneley Prince presented a paper entitled "A Modern Delaware Tale."

Messrs. Joseph Willcox, Joseph C. Fraley and Patterson Du Bois, the Judges of the annual election for Officers and Councillors, reported that the same had been held on this day, between the hours of 2 and 5 in the afternoon, there being present sixty duly qualified members, and that the following-named persons were elected, according to the laws, regulations and ordinances of the Society, to be the officers for the ensuing year :

*President.*

Isaac J. Wistar.

*Vice-Presidents.*

Coleman Sellers, Isaac J. Wistar, George F. Barker.

*Secretaries.*

I. Minis Hays, Edwin G. Conklin, Arthur W. Goodspeed,  
Morris Jastrow, Jr

*Treasurer.*

Horace Jayne.

*Curators.*

Charles L. Doolittle, William P. Wilson, William B. Scott.

*Councillors to serve for three years.*

George F. Edmunds, James T. Mitchell, Albert H. Smyth,  
Joseph Wharton.

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RESULTS OBTAINED FROM A SEARCH FOR THE TYPE  
OF NOCTUA LINN., AND CONCLUSIONS AS TO TYPES  
OF HÜBNERIAN NOCTUID GENERA REPRESENTED  
IN THE NORTH AMERICAN FAUNA.

BY A. RADCLIFFE GROTE, A.M.

(Read January 3, 1902.)

In view of the preparation of a general Catalogue of North American Lepidoptera, I have been asked to give the types of Hübnerian Noctuid genera. It is essential that systematists state the type of the generic title they use, and their work will be lasting in proportion as its literary basis has been proved. The scientific edifice will stand when the bricks are sound. A catalogue which employs the true, historically ascertained generic types has the advantage of possessing a permanent framework, even if later on the position of the objects designated be altered. And by using correct names a great advantage is secured to collectors and to literature. In my studies of the North American Noctuids for the

past forty years, I have had occasion to investigate the subject. The results, as to the types of our genera, are given by me in 1874, in the *Bull. Buff. Soc. N. Sciences*, and in the two following years in the *Buffalo Check List*; in 1895 in the *Abh. Naturw. Verein*, Bremen, also in the pages of the *Entomologist's Record*, London, England, Vol. vi, 27 *et seq.*; in 1900 in the *Can. Entomologist*, 209; also in publications of the *Ræmer Museum* and in these PROCEEDINGS.

In the present paper I have brought together the historical evidence as to the types of certain leading generic titles, often, perhaps commonly, used in a perverted sense, or given with a wrong authority. I have also investigated the question of the use of *Noctua* as a generic title in the Lepidoptera. I could not have attempted this latter without the kind aid of Mr. Jno. Hartley Durrant, of Thetford, England. The type here ascertained is *promuba*. The name *Noctua* is first used by Klein in 1753 for a genus of Mollusca. Linné introduced it then, in 1758, into the Lepidoptera in his combined term *Phalæna Noctua*. Fabricius follows with *Noctua* as a generic term in 1775, 1776-77, and claims the authorship. For those who reject any limitation for the application of the law of priority, its use in 1753 will prevent its being later employed in a different group of animals. It was not used in the Birds until 1809 by Savigny, a fact to which Boisduval drew attention in 1829.

In my late List (1895) of the North American Noctuids, I gave the ascertained types; what very few corrections have been found necessary are here made. The concluding portion of this List, embracing the *Catocalinæ* and *Hypeninaæ*, is not yet published. The unemployed terms in the Verzeichniss of Hübner need not be considered in the American Catalogue. They may be neglected until such time when the faunæ of Europe and America be so minutely compared, that subjective opinion can seize upon the smallest character for generic differentiation. As a rule, Hübner's genera in the Verzeichniss are of mixed contents, and I believe all having present application have been noticed by me.

In conclusion, I must thank Mr. Louis B. Prout, of London, England, and Mr. J. D. Alfken, of Bremen, for bibliographical assistance.



## NOCTUA.

LINNÉ, *Syst. Naturæ*, ed. x, Holmiæ (Salvii), 1758, *Phalæna Noctua*.

The "*Phalæna*" (496 footnote) are divided into seven groups, of which the "*Noctuæ*"—*antennis setaceis, nec pectinatis*—form the second. Linné gives the foot-structure of the larva of his "*Phalæna Noctua*" (497 footnote), so it seems reasonable, in a selection of the type, that this should be sought among the species whose larvæ he described. These are: *Phalæna Noctua strix*, *fagi*, *bucephala*, *humuli*, *dominula*, *fuliginosa*, *iacobææ*, *quadra* (this would be, however, excluded by Linné's *nota bene*), *pacta*, *pronuba*, *gamma* (not a "possible type" from Linné's remark—*Durrant i. l.*), *festucae*, *meticulosa*, *psi*, *chi*, *aceris*, *umbratica*, *exsoleta*, *verbasci*, *brassicæ*, *rumicis*, *oxyacanthæ*, *oleracea*, *pisi*, *atriplicis*, *præcox*, *triplasia*, *pyramidea*, *typica*, *delphinii*, *citrago*.

If we date the commencement of our nomenclature from Linné's tenth edition, the type of "*Phalæna Noctua*" should then be one of these. GEOFFROY makes no use whatever of *Phalæna Noctua* or of *Noctua*, simply using *Phalæna* with unnamed subdivisions (*Durrant i. l.*). The earliest restriction of the species of *Phalæna Noctua* brought to my notice is: *Poda, Ins. Mus. Græc.*, 88–91, 1761. The species there cited from Linné are: *Noctua iacobææ*, *quadra* (not a "possible type," *vide ante*), *dominula*, *pacta* (*Poda*, 90: this is not Linné's species, but is *nupta* Linné, therefore the name has no effect), *pronuba*, *gamma* (not a "possible type"), *exclamationis* (excluded, since Linné did not describe the larva), *?secalis*.

Of these species *iacobææ* is made the type of *Hipocrita* Hübn., 1806, *dominula* of *Callimorpha* Latr., 1810, and there would remain *pronuba* as the type of *Noctua*; *exclamationis* being congeneric with *segetum*, taken as type of *Agrotis* Hübn., 1806, and *secalis* being cited with a query. This latter is the same as *didyma* Esp., made the type of *Apamea* Ochs., 1816, through Duponchel, 1829. Before following the subsequent fate of *pronuba*, we will examine Linné's own restriction of his term *Phalæna Noctua*, which has given rise to the idea that the type of *Noctua* falls within the limits of Schrank's genus *Catocala*, the type of which I have shown to be *fraxini*, through Hübner's restriction in the *Verzeichniss*. This type covers our modern use of *Catocala* Schrank, 1802, which should in no case be disturbed. †

LINNÉ, *Mus. Ludov. Ultr. Reginae*, Holmiæ, 1764.

In this work Linné gives the following species: *Phalæna Noctua strix*, *punctigerata*, *fulvia*, *ornatrix*, *heliconia*, *rubricollis* (removed now to *Bombyx*, so that this species is excluded), *fraxini*, *pellex*. It is probable, from this restriction, the idea has arisen (communicated to me in letters) that *fraxini* was the type of *Noctua*, because *rubricollis* and *fraxini* are the only two of these species included by Linné in the *Fauna Svecica*, 1761, as Mr. Durrant writes me. Linné now, in 1764, excludes *rubricollis*, thus restricting the type to *fraxini*. But, since *fraxini* was not included by Poda in 1761, "this can be at once disregarded as of no effect."

CROTCH, *Cist. Ent.*, i, 61, 1872, writes:

*Noctua*—*N. sponsa* Lamark (1801). Cuvier and Latreille (1805) concur in this, but afterward Latreille (1810) selected *N. pronuba* as his type. With this selection the writer would be here agreed, and it remains to be seen what has been since done with *pronuba*.

#### TRIPHÆNA.

1816. OCHSENH., *Schm. Eur.*, iv, 69.

Interjecta, subsequa, comes (orbona), prosequa, consequa, lino-grisea, pronuba, fimbria, ianthina (ianthe, domiduca).

1816. HUEBNER, *Verzeichniss*, 221.

Interjecta, subsequa, comes, consequa, pronuba.

1829. DUPONCHEL, *Hist. Nat. Lep. Noct.*, Tom. iv, Pt. 2, 71.

Gives *pronuba* as the type of *Triphæna*. Therefore *Noctua* Linn., in the *Lepidoptera*, and *Triphæna* Ochs. would be synonymous, having same type. Mr. Meyrick (1895) uses *Triphæna* to the exclusion of this type. And this opens up the question as to the validity of the genus, which the type-seeker is not called upon to answer in the first instance. If *pronuba*, as being type of *Noctua*, could not be taken as type of *Triphæna*, then Mr. Meyrick's use of the latter term may be correct. This question does not seem necessary to answer for the North American Catalogue.

I now follow the use of *Noctua* by authors subsequent to Linné.

FABRICIUS, *Systema Entomologiæ*, Flensburgi et Lipsiæ, 1775.

In this work 122 species are enumerated under *Noctua*, pp. 590-619.

FABRICIUS, *Genera Insectorum*. . . . *Mantissa specierum*, Chilonii.

There is no date on title-page, but the Preface is dated Kilisæ, Dec. 26, 1776. This work is not given by Staudinger and Rebel, p. xviii, but is cited for *viminalis* with the date 1777. Fabricius quotes it, in 1781, as "Gen. Ins. Mant." It contains only six species under *Noctua*, but these are all new and constitute no restriction of those given previously. They are as follows:

(1) p. 282, *Noctua boleti*. This is *Scardia boleti*, a Tineid.

(2) p. 282, *Noctua virescens*. This appears to be the earliest description of the North American Noctuid *Chloridea virescens* Westw. ex Fab. and is neglected in the Washington Catalogue, 1893.

(3) p. 283, *Noctua roboris*. I cannot find this citation in Staudinger and Rebel. Reference is made to Roesel, I, tab. 50, and the insect there depicted may be *Dryobota roboris* B., Cat. I, No. 1821.

(4) p. 283, *Noctua monilis*. This appears to be the earliest description of the North American Noctuid *Hypsoropha monilis* Hübn. ex Fab., with a wrong locality, "Anglia."

(5) p. 283, *Noctua lanceolata*. The habitat is given as Germany. I cannot find the citation in Staudinger and Rebel.

(6) p. 284, *Noctua viminalis*. This is *Cleoceris viminalis*, referred incorrectly in the Catalogue, No. 1560, to *Bombycia*. The type of *Bombycia* Hübn., 1806, is B. or.

FABRICIUS, *Species Insectorum*, Hamburgi et Kilonii, II, 1781.

In this work 150 species are enumerated under *Noctua*, pp. 209-241. The six of the Gen. Ins. Mant. are included.

FABRICIUS, *Mantissa Insectorum*, Hafniæ, II, 1787.

In this work 309 species are enumerated under *Noctua*, pp. 135-184, and those previously described appear to be all carried forward.

In his *Genera Insectorum*, 1776, Fabricius cites "*Phalæna* Linn. Geoff." as equivalent to his genus *Noctua*, of which he evidently considers himself the author. Fabricius restricts *Phalæna* (p. 164, l. c.) to the Geometrids, using the term in a generic sense and citing Linn. Geoff. as authority. Following his own precedent he should here have applied Linné's term *Geometra*. Linné's "*Phalæna*," 1758, is evidently employed in a comprehensive sense, embracing all the seven groups: *Bombyces*, *Noctuæ*, etc. I have

made no search after the type of *Noctua*, Fabricius. It is evident he took the name from Linné, whether he credit it to him or not.

OCHSENHEIMER, *Schmetterlinge Europa's*, Vol. iv, 1816.

Ochsenheimer has no genus *Noctua*; *pronuba* is included by him in his genus *Triphæna*, with other yellow-winged Agrotids, differing in structure. On page viii, Ochsenheimer cites by its full title the Tentamen of Hübner, and says, literally: dieses Blatt kam mir erst lange nach dem Abdrucke des dritten Bandes zu Gesichte, daher konnte ich früher nichts davon aufnehmen. Already in 1876 I have shown that Hagen misquoted Ochsenheimer (*vide Buffalo Check List* and *Can. Ent.*), who in reality borrowed generic names and ideas from Hübner's Tentamen and properly gives him credit. Later writers, who are here so greatly indebted to their predecessors, could profitably take example.

Ochsenheimer's groupings of the Noctuids must be considered as expressing his idea of their affinities, because on page ix he says that he only catalogues and describes what he could compare in nature, not relying upon descriptions or figures, and that his systematic list is at the same time the catalogue of his collection. He gives no descriptions of his genera, any more than Hübner in the Tentamen.

BOISDUVAL, *Europæorum Lepidopterorum Index Methodicus*.

Dated on title-page 1829, but the Preface is dated Sept. 30, 1828. The work has priority over Duponchel's volume, March, 1829, or Curtis, May, 1829. "*Noctua mihi*," p. 63, contains names of some 70 species; Boisduval cites "*Agrotis et Noctua Treits*," and "*Agrotis et Graphiphora Ochs*," as synonymous. The type of *Agrotis* Hübn., 1806, *segetum*, is included. "*Triphæna* Ochs. Treitsch.," p. 68, contains 7 species, among them *pronuba*, designated by Duponchel as type.

After Fabricius, the responsibility for the use of *Noctua* mainly rests with Boisduval. I cannot find that Hübner ever used the term in a generic sense.

BOISDUVAL, *Genera et Index Methodicus*.

Dated on title-page and in Preface 1840.

"*Triphæna* Treits. Boisd." contains 8 species, among them Duponchel's type.

*Opigena* Boisd., 1840, monotypic for *polygona*.

*Chersotis* Boisd., 1840, with 8 species.

"*Noctua* Treits.," *sagittifera* and 18 other species.

*Spalotis* Boisd., 1840, for *augur* and 22 other species.

"*Agrotis* Ochs. Tr.," *agricola* and 36 other species, including *exclamationis*, designated by Duponchel in 1829 as the type of *Noctua*, but erroneously so, since this is taken by *Agrotis*, 1806, being congeneric with *segetum*. It is also excluded by Durrant as being unknown in the larval stage to Linné.

SPEYER, in the second edition of Dr. Schenckel's *Schmetterlings-sammler*.

Undated, Mainz, C. G. Kunze. Has a genus "*Tryphæna*," as used by Ochsenheimer and Boisduval, and employs *Opigena* for *polygona*. In late editions, undated, of his popular book, "*Schmetterlingskunde*," Speyer continues to use *Tryphæna* (*Triphæna*) in Hübner's sense, and includes *pronuba* in its second section. These authors, therefore, regarded *Triphæna* as a distinct genus from *Agrotis*. Since I have not found in the N. Am. Noctuid fauna the precise structural equivalent of *pronuba*, it may not be necessary for the American Catalogue to use either *Triphæna* or *Noctua*. *Agrotis gilvipennis* Grote, referred by me in 1890 to *Triphæna*, belongs, I believe, having no specimen at present, to *Lampra*. It remains for the systematist to decide what species, other than *pronuba*, can be taken as type of *Triphæna*. Duponchel's type, *pronuba*, can remain, if my view that *Noctua* is untenable obtains.

LEDERER, *Noctuiden Europa's*, Wien, 1857.

Lederer has no genus *Noctua*, the species here regarded as typical being referred to one of the sections of *Agrotis*. Lederer divides the numerous species of *Agrotis* primarily upon secondary sexual characters, the male genitalia. Already, in 1874, I had proposed to divide the species into two chief groups—those species which had all the tibiæ spinose and those in which the middle and hind tibiæ alone are armed (*Bull. Buf. S. N. S.*, 11). Subsequently, in the *Canadian Entomologist*, I proposed a further addition, including the genus *Carneades*. This classification of mine gives three principal divisions for the North American species:

Front smooth, fore tibiæ unarmed: *Epilectra*, *Lampra* Hübn.

Front smooth, fore tibiæ armed: *Triphæna* O., *Agrotis* Hübn.

Front tuberculate, fore tibiæ armed: *Carneades* Grote.

Lederer makes, I believe, some structural misstatements. He gives the male antennæ of *linogrisea* as "pyramidal zähnig." This species is the type and sole species of *Epilectra*. Its diagnosis should read: Thoracic vestiture scaly; male antennæ simply brush-like, nearly naked; fore tibiæ unarmed; front smooth. The eyes, as in all these structures, naked. Lederer further gives *agathina* as having the fore tibiæ armed and triangulum unarmed, whereas the reverse appears to be the case. In *depuncta* the thoracic vestiture seems scaly, whereas Lederer places it in a section where this is hairy. Neither *Epilectra* or *Triphana* (*Noctua* L.) need apparently affect the American Catalogue. The species referred in the "Revision" to *Noctua* belong to *Amathes*. Lederer's neglect of Hübner and his uncritical use of several generic names has increased the confusion, which is the more to be regretted since his structural observations are usually so valuable.

To sum up: There seems no use in disturbing Duponchel's type, *pronuba*, for *Triphæna*, until it is settled whether the term *Noctua* Linné can be employed. I conclude that the historically indicated type of *Phalæna Noctua* Linné is *pronuba*, and that the term *Noctua* cannot be used in the Lepidoptera because preoccupied by Klein in the Mollusca in 1753. The earliest plural form I find, which could be used, outside of *Noctuæ*, for the family is *Apatelæ* Hübner, 1806, and the family type would be *Apatela aceris*. The name *Agrotidæ*, H.-S., based on *Agrotis* Hübn., 1806, which latter occurs on the same page, is a more appropriate title for the whole group in Lederer's sense. Lederer himself gives no scientific title to the group. In the present case, if we exclude the term *Noctua*, there can be no doubt that the leading genera of the group are: *Apatela*, *Agrotis*, *Hadena*, *Cucullia*, *Plusia* and *Catocala*. Three of these belong to Schrank, 1802, and three to Hübner, 1806. Hübner's names have the preference for a family title, because he employs also the plural form, with the evident intention of using them for comprehensive groups, an intention he carries out ten years later, in 1816, in the *Verzeichniss*.

Taking the opposite conclusion, that *Noctua* Linn. is a valid generic title, its type being *pronuba*, then the question comes up: Is *pronuba* congeneric with *Agrotis segetum*? If so, then *Agrotis* falls before *Noctua* Linn. Meigen (1832) includes 155 species under *Noctua*, with *Hadena*, *Orthosia*, etc., as subgenera. His subgenus *Noctua* contains *baja*, *candelisequa*, *brunnea*, *festiva*, *rhombsidea*,

gothica (!), *C. nigrum*, *triangulum*, *flammatra*, *musiva*, *plecta*, *punicea*. He remarks: der Rücken hat einen Schopf. In the main this seems to be the group intended by Prof. J. B. Smith as *Noctua*, but it cannot include either *pronuba* or *segetum*. Meigen places the latter correctly under the subgenus *Agrotis*, but classifies *pronuba* under the distinct genus "*Tryphæna*" section A, which he characterizes as having the third palpal joint reduced, hardly noticeable. It does not seem as though subjective opinion would ever rest content with the reference of *pronuba* as congeneric with *segetum*, and therefore the question of the genus *Noctua* need not affect the North American Catalogue.

At the present time the study of the Noctuids in America is suffering under the evil duplication of specific names and a reckless disregard of the historically indicated types of the generic titles. In this connection may I ask how *Noctua* comes to be applied to the group in Prof. Smith's Revision, except by a kind of restriction? For Linne's original *Phalæna Noctua* contains insects belonging to several distinct families and only by some sort of literary precedent has it come to designate Owlet Moths or Noctuids. The same sort of historical research, only carried out with more exactness, reveals the types I must insist upon for certain genera. And, unless it can be shown, in any special instance, that I have erred (the study has often proved intricate), it will be clearly to the advantage of science that my results be adopted in the new N. Am. Catalogue. I now give here references I have made and the types which they reveal:

#### MAMESTRA.

1816. OCHSENH., *Schm. Eur.*, iv, 76.

*Pisi*, *splendens*, *oleracea*, *suasa*, *aliena*, *abjecta*, *chenopodii*, *albi-colon*, *brassicæ*, *furva*, *persicariæ*.

1816. HUEBNER, *Vers.*, 214.

*Pisi*, *unaminis*, *leucophæa*. Under this restriction *pisi* became type, since Hübner's two other species are not included originally.

(March) 1829. DUPONCHEL, *Hist. Nat. Lep. Noct.*, T. iv, Pt. 2, 71.

Designates *brassicæ* as type, but this restriction of *Mamestra* is no longer possible since Hübner's action in the Verzeichniss. Hübner must have taken this generic name from Ochsenheimer,

1816; hence this part of the Verzeichniss must be of later issue, probably 1822, but at any rate earlier than Duponchel.

1874. GROTE, *Bull. Buff. S. N. Sci.*, 12.

Lists the N. Am. species and takes *pisi* as type. This accords in a general way with the modern definition of Mamestra: Hadenoid forms with hairy eyes, the non-extruded ovipositor and different larval habit separating them from *Hadena* (type *cucubali*) Schrank non Lederer (= *Dianthœcia* Bois.). I list the North American species of *Dianthœcia*, for which name *Hadena* Schrank must now be substituted, and give the characters in Rev. Check List, N. Am. Noct., 1890, 13 (Bremen, Homeyer & Meyer).

#### HADENA.

1802. SCHRANK, *Fauna Boica*, II, 2, 158.

Refers to this genus the species of his families M. and N. These species are: *typica*, *atriplicis*, *pisi*, *oleracea*, *chenopodii*, *præcox*, *xanthographa*, *piniperda*, *deaurata*, referred to family M, and *meticulosa*, *lucipara*, *cucubali*, referred to family N. One of these twelve Noctuids must then be the type of the name of *Hadena*. According to modern views species 1, 2, 8, 10 and 11 are monotypic, 3-5 are Mamestrians, 6-7 Agrotids. The contents are much mixed, referable to nine genera.

1816. OCHSENH., *Schm. Eur.*, iv, 70.

Excludes all the species of Schrank's family M, but includes all of N, among his 29 species of *Hadena*. The mixture is now more frightful than it was at first. The three original species of *Hadena*—*meticulosa*, *lucipara* and *cucubuli*—are, however, included, and one of these three must now be the type. It is noticeable, however, although species with hairy and naked eyes are indifferently cited, that all the species of *Dianthœcia* are included by Ochsenheimer.

1816. HUEBNER, *Verzeichniss*, 216.

This part of the *Verzeichniss* is of later date than Ochsenheimer's volume. Hübner includes under his genus *Hadena* only two of Schrank's original species, *typica* and *cucubali*. The first is excluded by Ochsenheimer's first restriction in 1816, and moreover became the type of *Nænia* Stephens in 1829. *Cucubali* becomes, therefore, the type of the genus *Hadena*, and is to be looked upon



as the original "Trübeule." It is unnecessary, having found the type, to follow the fortunes of *Hadena* further. It was used improperly by Lederer for a large genus of naked-eyed species separable from *Mamestra* on this character.

1895. GROTE, *Ent. Record*, vi, 78.

Designates cucubali as type of *Hadena*, and states that *Dianthacia* Boisduval, will probably prove synonymous.

#### XYLENA.

1806. HUEBNER, *Tent.*, 1.

*Lythoxylea* (*lithoxylea*) sole species and therefore type.

1816. OCHSENH., *Schm. Eur.*, iv, 85.

Vetusta, exoleta, conformis, lapidea, rizolitha, petrificata, conspicillaris, patris, spinifera, scolopacina, rurea, hepatica, polyodon, lateritia, lithoxylea, petroriga, pulla, cassinea, nubeculosa, pinastri (scabriuscula), rectilinea, ramosa, lithoriga, hyperici, perspicillaris, platyptera, antyrrhini, linariæ, opalina, delphini. Ochsenheimer quotes Hübner and spells the genus as he does, *Xylena*. This is the worst of Ochsenheimer's mixtures and, while enlarging Hübner's genus, the beginning of all subsequent confusion in applying this generic title. This abuse is still being perpetuated, although I gave again the type in 1876. Later writers than Ochsenheimer take out the Lithophanoid forms (Fam. A in part, petrificata, etc.), and use for them a genus "*Xylina* Ochs. or Tr.," whereas Ochsenheimer has no generic term so spelled. They then reject the Hadenoid forms (Fam. B in part), which include Hübner's type lithoxylea, instead of the reverse. Hübner himself, in the *Verzeichniss* refers lithoxylea to the same group as petrificata, and the truth seems to be that, perhaps up to Stephens, the generic types I now give to *Xylena* and *Lithophane* were thought congeneric or nearly allied. The genus *Xylophasia* Stephens is a synonym of *Xylena* Hübner, having the same type.

(1828) 1829. BOISD., *Eur. Lep. Ind. Meth.*, 86.

Cites "*Xylina* Tr. and *Xylena* Ochs.," and suppresses Ochsenheimer's reference to Hübner for the term.

(March) 1829. DUPONCHEL, *Hist. Nat. Lep.*, iv, Pt. 2, 72.

Gives vetusta as type, but this is impossible.

1876. GROTE, *Buff. Check List Noct.*, 37.

Restores Hübner's type and spelling, and gives *Hadena* (Lederer nec Schrank) as identical. The type of Schrank's genus was not then ascertained.

I show, in 1874, that the modern genus "*Xylina*" must be called *Lithophane* Hübn., 1816, with the type *socia* (petrificata)—a far more appropriate name.

The American species referred to *Hadena*, Lederer nec Schrank, should be catalogued under the following genera: *Xylena* Hübn. (= *Xylophasia* Steph.), type *lithoxylea*; *Helioscota* Grote, type *miselioides*; *Oligia* Hübn. (nec Grote, Smith), type *strigilis*; *Pseudanarta* Grote, type *flava* (crocea); *Monodes* Guen. (= *Oligia* Auct. nec Hübn.), type *nucicolor* (paginata). A very good notice of the species of *Monodes* will be found in *Entom. Am.*, Vol. v, p. 145, under the name *Oligia*. It may be said of all these genera, what is there said of *Monodes*, that they are not "strongly characterized." They have in common naked eyes, unarmed tibiae, smooth clypeus and hadeniform cut of wing. *Xylena* may have a strong character in the thoracic shield of the larva. The species belonging to these genera vary from being robust, hairy and tufted down to sligher, scaly and smoother forms. To *Xylena* belong species like *lignicolor*, *auranticolor*, *genialis*, *cristata*, *vulgaris*, *verbascoides*, *cuculliiformis*, *hulsti*, *vultuosa*, *sputatrix* (I do not acknowledge this to be Walker's *dubitans*), *devastatrix*, *occidens*, *arctica*, *violacea*, *Bridghami*, *apamiformis*, *lateritia*, *suffusea*, *remissa*; to *Helioscota*: *miselioides*, *marina*, *chlorostigma*, *mactata*, *modica*, *diversicolor*. From want of space and material I do not carry these references further here.

## APAMEA.

I proposed at one time to take Ochsenheimer's *nictitans* as type of *Apamea*, it is his first species; this *nictitans* is not the *Gortyna nictitans* L. of Lederer, but is *nictitans* Esp., a variety of *secalis* L. = *didyma* Esp. = *oculea* Guen. (*Cat. Staud. and Rebel*, p. 175). My reference was correct, for this species had become type of *Apamea* through Duponchel in 1829. The similarity of the name led me, however, to mistake Ochsenheimer's species for *nictitans* Bkh. (given by Lederer as of Linné) = *chrysographa* Hübn. (*Cat. Staud. and Rebel*, p. 186), which latter is the type of *Hydræcia* Guen., as shown by me in these pages and elsewhere. It is

probable we have N. Am. species congeneric with *didyma* (*secalis* L.), but at this writing I cannot indicate them. Lederer's restriction of *Apamea* to *testacea*, which I followed in 1895, should not be accepted; this is the true type of *Luperina* Boisd. (see Grote, *Can. Ent.*, 1900, 211). Boisduval, in 1829, refers both *nictitans* (*chrysographa*) and *nictitans* (*didyma*) to *Apamea*.

## PSEUDANARTA.

1878. GROTE, *Bull. U. S. Geol. Surv.*, 178.

*Crocea* (*flava*), sole species given and therefore type.

1882. GROTE, *New Check List*, New York, 27.

*Flava*, var. *crocea*, *singula*, *flavidens*, *aurea*. The name, without citation, is credited to Hy. Edwards, under the mistaken idea, derived from correspondence, this author had used it. *Pseudanarta* was originally proposed by Grote in letters to Hy. Edwards for this author's *Anarta crocea*.

1889. J. B. SMITH, *Ent. Am.*, v, 175.

*Falcata*, *aurea*, *flava* (*crocea*), *singula*, *flavidens*. The genus is credited to Hy. Edwards and the citation: "Proc. Cal. Ac. Sci., Vol. 6, p. 133, 1875," is supplied. But this page contains the original description of *Anarta crocea*, and the name *Pseudanarta* does not occur in any of the communications of Hy. Edwards to the California Academy: "Pacific Coast Lepidoptera, Nos. 1 to 22," all published. This erroneous citation is twice repeated in the Washington Catalogue, 148, 1893.

1895. GROTE, *Abh. Naturw. Ver. Bremen*, xiv, 37.

*Flava*, var. *crocea*, *singula*, *flavidens*. The genus is limited to these three species; *falcata* and *aurea* are excluded, owing to Prof. J. B. Smith's remark on their tibial structure in 1893.

## COPANARTA.

1895. GROTE, *Abh. Naturw. Ver. Bremen*, xiv, 70.

*Aurea*, *falcata*, *aterrima*; *aurea* specified as type.

## PLUSIA.

1806. HUEBNER, *Tent.*, 2.

*Chrysitis*, sole species and therefore type. This name is erroneously given to Ochsenheimer, who however cites Hübner's *Tenta-*

men and includes his type. Lederer in 1857 cites *Plusia* Fabr., but I can find no such genus in Fabricius and the name should be restored to Hübner. *Chrysoptera* Latr., 1825, is said to be preoccupied. It is used by Meigen in 1832 for *concha*, *deaurata* and *moneta* alone.

The names and types of the subgenera of *Plusia* are given by me in these PROCEEDINGS, 417 (1895). Typical N. Am. species of *Plusia* are: *derea*, *dereoides*, *balluca*, *metallica* (*lenzi*, *scapularis*).

#### GRAPHIPHORA.

1806. HUEBNER, *Tent.*, 1.

Gothica, sole species and therefore type.

1816. OCHSENH., *Schm. Eur.*, iv, 68.

Ravida and sixteen other species belonging to *Agrotis* in sensu Lederer, excluding Hübner's type, though taking the name from Tentamen. The confusion now commences in European literature. The genus is used for Agrotidians, with which gothica was originally held as allied, until the type is made also the type of *Tæniocampa*, Guenée, which must fall.

1816. HUEBNER, *Verzeichniss*, 220.

Has no genus, but a Stirps *Graphiphoræ*, which comprises numerous genera, mostly of Agrotidians, among them *Epi-sema*, which he takes from Ochsenheimer, including gothica. No examination had been made then of the structure of the eyes and legs; pattern and size seemed at that time to warrant the juxtaposition of *Tæniocampids* and Agrotidians (still difficult to separate, *e. g.*, *Pachnobia* and *Metalepsis*). But the original sense of *Graphiphora* must be restored. Boisduval, in 1829, refers "*Graphiphora* Ochs." as a synonym of *Noctua* and *Agrotis*, and includes its type gothica (*l. c.*, 67) as structurally identical. This proves the accuracy of the statement given above as to the views prevalent at the beginning of the last century.

1875-76. GROTE, *Buffalo Check List*, 13, 37.

Gives the North American species, referred to *Tæniocampa*, to *Graphiphora*, and designates gothica as type. Repeats this in 1895, *Entom. Record*, 29, and last Check List, *Abh. Brem. Nat. Ver.*, xiv, and now "finally" insists.

## XANTHIA.

1806. HUEBNER, *Tentamen*, 1.

Fulvago (puleacea), sole species and therefore type.

1816. OCHSENHEIMER, *Schm. Eur.*, iv, 82.

Luteago and sixteen other species. Cites Hübner, but includes his type under *Cosmia*. The similar endings of the names of the yellow autumnal species, in *ago*, may have helped to increase the confusion in their application which prevails in early European literature. Hübner's erroneous use of "fulvago" may have led to his generic title being misapplied. Species of *Citria* and *Orthosia* are constantly referred in America to *Xanthia*, which term should be kept in the North American Catalogue for *paleacea* alone, specimens of which I described under the name of *infumata*, not knowing the European species, now believed to be identical with our own. *Enargia* Hübn. Verz. has *paleacea* also for type and falls before *Xanthia*.

## COSMIA.

1806. HUEBNER, *Tentamen*, 1.

Affinis, sole species and therefore type.

1816. OCHSENH., *Schm. Eur.*, iv, 84.

Fulvago (W. V. Hübner = *paleacea*), *gilvago*, *abluta*, *trapezina*, *diffinis*, *affinis* and *pyralina*. Cites Hübner's *Tentamen* and includes his type of *Cosmia*. The genus should be restored to Hübner, but has no place in our American Catalogues. Ochsenheimer corrects Hübner's erroneous application of "fulvago."

## AMPHIPYRA.

1816. OCHSENH., *Schm. Eur.*, 70.

*Tragopoginis*, *tetra*, *livida*, *cinnamomea*, *pyramidea*, *perflua*, *spectrum*.

1829. BOISD., *Eur. Lep. Index Meth.*, 68.

Uses it for the same species. The first six species belonged since 1806 to *Pyrophyla* (r. *Pyrophila*), and the type of *Amphipyra* is *spectrum*. The genus is not represented in America. Our species belong to *Pyrophyla* Hübn., 1806, type *pyramidea*.

## ACONTIA.

1816. OCHSENH., *Schm. Eur.*, iv, 91.

Malvæ, aprica, caloris, titania, solaris, luctuosa.

1816. HUEBNER, *Verzeichniss*, 257.

Malvæ, sole species and henceforth the type.

1895. GROTE, *Entom. Record*, 79.

Designates malvæ as type through Hübner's restriction. This part of Hübner's *Verzeichniss* is of later issue than Ochsenheimer's volume, from which Hübner takes such genera as *Acronicta*, *Mamestra*, *Triphana*, etc. The genus *Acontia* should not be used by the American Catalogue, as it is confined to Europe. Our species belong to *Tarache*.

## TARACHE.

1816. HUEBNER, *Verzeichniss*, 261.

Caloris (caffraria), solaris, insolatrix (ined.), aprica, opalina.

1874. GROTE, *Bull. B. S. N. S.*, 36.

Designates aprica as type.

## ERASTRIA.

1806. HUEBNER, *Tentamen*, 2.

Amataria, sole species and therefore type. This is a genus of Geometrids and the name is erroneously applied by Ochsenheimer to a genus of Noctuids. Its use should be avoided by every careful and unprejudiced person in the Noctuids for this very good reason.

## EUSTROTIA.

1816. HUEBNER, *Verzeichniss*, 253.

Unca, sole species and therefore type. The North American Noctuids referred to *Erastria* belong to this genus, which is used in the Catalogue of 1874, *Bull. Buff. S. N. S.*, 37, and subsequently. The change back to *Erastria* in the Washington Catalogue is inexcusable.

## EUCLIDIA.

1806. HUEBNER, *Tentamen*, 2.

Glyphica, sole species and therefore type.

1816. OCHSENHEIMER, *Schm. Eur.*, iv, 96.

Monogramma, glyphica, triquetra, mi. Cites Hübner's *Tentamen* for name and includes his type. Ochsenheimer gives no generic description, and yet he is constantly cited as author. Hübner's property should be restored to him.

#### LITOGNATHA.

1873. GROTE, *Bull. Buff. Soc. N. S.*, 85.

Nubilifascia, sole species and therefore type.

1895. GROTE, *Proc. Am. Phil. Soc.*, 429.

Nubilifascia, cribrumalis. This generic name is referred in the Washington Catalogue to Hormisa Walker, but Walker's original specimen over this label we saw in 1867, and it was a specimen of *Epizeuxis æmula*. This determination is supported by the text of Walker's description of the genus Hormisa, which agrees with *Epizeuxis* and absolutely contradicts Litognatha. Litognatha should be restored.

#### ZANCLOGNATHA.

1857. LEDERER, *Noct. Eur.*, 211.

Tarsiplumalis, tarsicrinalis and others.

1895. GROTE, *Proc. Am. Phil. Soc.*, 424.

Tarsiplumalis, tarsipennalis and others. Tarsiplumalis may be taken as type, as stated in Buffalo Bulletin, 1874.

ROEMER MUSEUM, November, 1901.

### A MODERN DELAWARE TALE.

BY J. DYNELEY PRINCE, PH.D.

(Read January 3, 1902.)

The chief differences between the two ancient dialects of the Lenape, viz., the Unami-Unalachtigo and the Minsi, have been pointed out by the late Dr. Brinton (*The Lenape and their Legends*, pp. 91ff.). Both these varieties of Delaware speech are still in use in a modern form—the Unami-Unalachtigo by the descendants of the Delawares who now occupy lands in Indian Territory, in the

Muskogee Agency of the Cherokee Nation, and the Minsi by about three hundred Indians in Ontario, Canada, viz., one hundred at Munceytown, one hundred at Moraviantown, the seat of a Moravian mission, and the same number at Hagersville, on the Six Nations' (Iroquois) Reserve. There are also a few Minsis at New Westfield, near Ottawa, Kansas, most of whom are under the charge of the Moravian Church.<sup>1</sup>

The following witchcraft story in the modern Minsi was sent to me, with other MS. material, by Mr. Nelles Montour, Chief of the Minsis at Hagersville, Ont., a well-educated Indian who writes his own language with great clearness. Like all Indian scribes, however, Chief Montour writes syllabically, separating the syllables of his texts and not the words, a process which makes a correct edition of his MSS. extremely difficult. For example, in the following tale in II.<sup>b</sup> Montour wrote *keerh keeth qta*, as three distinct syllables. This resolves itself under analysis into *keerhkee th'q'ta* 'by the fire.' His translation also is in many instances so free as rather to obscure the true meaning of the original. Thus, in IV.<sup>c</sup>, he renders *chee quack leetahhawa dulwihkawawh* 'I am a greater man than he.' The correct translation is undoubtedly 'Do not think about it; I will overcome him.' Then, too, the not always uniform, cumbrous English system of spelling followed by Montour, in common with those of his tribe who are members of the Church of England, makes an accurate analysis of his texts doubly trying. The English values of the consonants probably do not reproduce the Indian sounds with great exactness, as may be seen from Montour's constant use of the spelling *quack* 'what,' which clearly should be written *queq* (see below on III.<sup>b</sup>), as well as from his consistent omission of the *n* prefix of the first person before *g* and before the intercalary *-d-*, as in *gutauch*, I.<sup>c</sup>; *dilnoom*, III.<sup>b</sup>, etc. The Moravian Minsis still use the much more appropriate German system of phonetics.

The analysis of the following tale has been made chiefly by means of the Old Delaware materials left by the German Moravian missionaries of the eighteenth century, tabulated in a convenient form by Dr. Brinton in his *Lenape-English Dictionary*.<sup>3</sup> In cases

<sup>1</sup> These details were furnished by Chief Nelles Montour, of Hagersville, Ont., and by Mr. Dew M. Wisdom, formerly Indian Agent at Muskogee, I. T.

<sup>2</sup> *A Lenape-English Dictionary*, by Daniel J. Brinton, A.M., M.D., and Rev. Albert Seqaqkind Anthony, Philadelphia, 1888. The material is drawn from a MS. dictionary preserved in the Moravian archives at Bethlehem, Pa.



where the Minsi deviates greatly from the mixed Unami-Unalachtigo dialect, in which the missionaries wrote, I have had recourse to the vocabularies of the cognate Abenaki and Ojibwe languages,<sup>3</sup> which have given fairly satisfactory aid in every instance save one (in V. <sup>b</sup>). The chief phonetic variation between Montour's dialect and the language of the Moravian missionaries is the appearance of *th* (soft, as in 'this') in Minsi as representing *s* in Unami-Unalachtigo; cp. *wsheettha* for O. D. *w'schiessa* 'his uncle,' the ending *-multhoo* for O. D. *-mallsin*, etc. Brinton asserts (*Dict.*, p. vi) that this *s* in O. D. was due to the fact that the Germans were unable to distinguish the soft *th*, which they accordingly represented by *s*. Thus Anthony, Brinton's native authority, states (*Dict.*, p. 115) that the common word for 'boy' in his language is *skahenso*, which appears in Montour's text in the form *thkuhinthoowh*, IV. <sup>a</sup>, representing the actual pronunciation. Furthermore, in the letter from Chief Gottlieb Tobias (*Len. Legends*, p. 88) we find the form *lichsoagan* 'language,' which Montour would write *leerhthoowawgun*. In other words, those Indians who read the language according to the German system lisp the *s*.

In the following modern Minsi text these important points with regard to the pronunciation should be noted: 1. Medial and final *h* is never an aspirate, but merely a pause. 2. The combination *ng* is pronounced like *ng* in 'king.' 3. The combination *rh* is a deep guttural *gh*. Actual *r* has not existed in Lenape since the days of the early Swedish colony in Pennsylvania and New Jersey. It is now represented by *l* as in modern Abenaki (*l* = ancient *r*). 4. *W* before another consonant is pronounced, as in Passamaquoddy, with a short unclear vowel following it, similar to the Hebrew *Sh'va mobile*. 5. *Wh* is a guttural combination composed of *w* + *kh*. 6. The apostrophe (') indicates a very short *u*. 7. The vowels are to be pronounced exactly as in English.<sup>4</sup> The O. D. words are written entirely according to the German system. The Abenaki vowels are pronounced as in Italian, except the *ø*, which has the sound of the French nasal *on*. The sign ' indicates a soft guttural voice-stop similar to the Arabic medial *He*. The vowels

<sup>3</sup> The Abenaki material is drawn from a dictionary of the modern dialect now in course of preparation by myself, and the Ojibwe words are taken from Baraga's *Dictionary of the Ojibwe Language*, Circinnati, 1853.

<sup>4</sup> Cp. Prince, "Notes on the Modern Minsi Delaware Dialect," *Amer. Journal of Philol.*, xxi, pp. 295-302.

in the Ojibwe words have the Italian and the consonants the English values.

The subject matter of Montour's tale is interesting, dealing as it does with cannibalism, a vice which was unknown among the Algonquin tribes, except in the case of wizards. In this particular story it should be noticed that the spirit *Muttontoe* (the Abenaki *Madahôdo* 'Devil') desires to devour an *aged man*. This may be a survival of the primitive time when it was actually the custom to eat the old people, apparently in order to get rid of them, as has been the case until quite recently among the Tierra del Fuego tribes. It is at least curious that the *Muttontoe* desires to eat the elderly rather than the young man, who would be a better subject for mere cannibalism. It is also very striking that the uncle becomes *sick* first and thus incapacitated. This would seem to indicate a survival of some archaic idea, concealed here under the veil of a witchcraft superstition, that the *old man* was the proper prey for the man-eater. This tale seems to embody a different principle from that shown in the Passamaquoddy account of two wizards who retired to an isolated island (Grand Manan) to devour the body of a man.<sup>5</sup> In the latter instance, the cannibalism was of the ordinary sacramental character, viz., the cannibals hoped to absorb some of their victim's mental qualities by devouring his flesh. It is not impossible that the custom of eating grandparents and other aged incapable persons might have had for its basis a similar sacramental idea—i. e., that the old people, by entering the bodies of their descendants, should live again and at the same time impart to the younger cannibals some of the nature of the aged victims.

As literature in modern Delaware is so rare, I have given a careful philological analysis of Montour's tale, so far as my imperfect knowledge of the language has permitted.

#### WITHKEELNO WAUK WSHEETHA.

I. \*Weekwaum lawee kohpe weekena withkeelno wauk wsheetha mahji kihkweelno wrhalin neepnumo. <sup>b</sup>Tah lickee wsheetha weenamulthoo, oonjeemawuh

#### A YOUTH AND HIS UNCLE.

I. \*In a wigwam in the midst of the forest lived a youth and his uncle of many summers. <sup>b</sup>Once upon a time the old man was taken ill (and) called his nephew

<sup>5</sup> See Prince, PROC. AMER. PHILOS. SOC., xxxviii, pp. 182, 184, nr. v.

wlunquathitha aleh-mawmjeenah kihlkoolaut. \*Withkeelno lawalindum, leetahah: "gutauch wutchawha jeeth. <sup>a</sup>Noolihtoomich mihtqueenootee wauk kpuheekun waukitch nooshwuhtoonich uhpeeyuhk nahtau aleenawqtheet." \*Waupungeek andah-keshihtootah mihtqueenootee meelaun. Wsheethaha wlalindumoo wekwulup laulpuksho. <sup>f</sup>Nulhuh-nuh wtuhlaun wsheetha ahpeewuyuhpeenang. \*Waupungeeka weenumultheet ithpeenurhka aleet "klithtuh." <sup>b</sup>Wtilawul withkeelno: "ahwanitch pawhji; cheepeenawqthoo wauk ahkonjauptoona kweeshulookich, shuqk chee weeshulookoowih; muthkuneetahaul; pawoich andah-laweetpihkahk andah-wam-quack-kaweeet."

II. \*Nulnuh peethkahkeek andah-mahji-keeshmeettheeteetah, withkeelno awuthee tindawing lmutawpoowh, pahtoon tah nij alak nih aleetpihkahk. <sup>b</sup>Weerh-kawa quack konjwah wuhkoong; ahwan cheepeenawqthoo wcherh-akahlaun keerhkee th'q'ta: "Ugh," owh, "baum konjahwan nhukee; nmihwa linno. Ktuhaulaw ksheeth; naulaw; Ugh, kweeshathee." <sup>a</sup>Withkeelno mutahkawh weelno, shuqk wun keemoorh konjahwan weeshulooko nawkawh. \*Nul muthkuneetaha neepahwooh; owh:—"Mawhah geesh-keeshajpinah-

to say to him his last words. \*The young man grieved (and) thought thus:—"I will make everything comfortable for my uncle. <sup>a</sup>I will construct a basket with (lit. and) a lid, and I will put in it all kinds of downs." \*On the morrow, when he had finished the basket, he presented it. His uncle was pleased and received it weeping (*i. e.*, with gratitude). <sup>f</sup>He then placed his uncle in the soft downy bed. \*On the morrow, the sick man stretched out his hand which meant "attention." <sup>b</sup>He told the youth (then):—"Some one is coming at whose terrible appearance and condition thou shalt be terrified, but fear not; take courage. He comes in the midnight hour when all things are sleeping."

II. \*On that same night, after they had eaten, the youth sat on the opposite side of the fire, awaiting the outcome of that night. <sup>b</sup>Suddenly there was something overhead and a certain terrible-looking being dropped down by the fire: "Ugh," said he, "I myself am here; I eat man; thou lovest thine uncle; I want him; Ugh, thou fearest me." <sup>a</sup>The youth had fought with wild animals (?), but this wizard, as he must be, frightened him for a while. \*Then, summoning his courage, he stood up on his feet

wa." Owh yohquh:—"Law-  
peewhich baum; keeshajpina-  
witch." 'Nul ktithpihlaun aleen-  
qahtang.

III. \*Nul withkeelno lmutah-  
poowh lawpeewh wtilawul whu-  
kee yul:—"Kalahaat cheepah-  
wan. Shurhke kalahnickulooq-  
kich jeeth. Quackwichha dil-  
noom? Dulmitheemich ahlih-  
wthihkaw, tauthrha ahwana-  
wah." \*Withkeelno uhloomth-  
oowh, shuqk wtilawul wsheethul:  
—"Lawpeewhich baum."

IV. \*Aloorhwat quack, yih  
weekwaum thkuhinthoowh pat-  
chihkcheewh; owh:—"Taunha  
wtindin ksheeth?" <sup>b</sup>(Mawsha-  
lindum) Mawsheelahwahkoo  
almawsheel wam wawihtoon ay-  
lackwloowheen. \*Wauk uhloom-  
thoowh wauk lawpeewh moorh-  
kum weekwaum ahwawhlikqoo  
shawa wninahko wtil-sheewa-  
lindumoo weenawqthowh. <sup>d</sup>Nul  
wam wtilauch mookahwaun.  
Wtil wturhquon cheepahwan.  
Shawa wninootumin wuh linno  
nunrhat Muttuntoe. \*Nul wtil-  
awul withkeelno: "Chee quack  
leetahhawa dulwihkawah. Ktilil  
yoonich ktilnumin wauk ktilooh-  
moolin wanjich ahloowhweekah-  
wut."

and said:—"I cannot have him  
ready." Again said (the wiz-  
ard):—"I shall come here once  
more; let him be ready" (then).  
'Then he leapt up through the  
smoke-hole.

III. \*The youth sat down  
again and spoke thus with him-  
self:—"Truly he is awful. It  
must be that my uncle shall  
leave me. What am I to do?  
I will go toward the setting sun.  
(Perhaps) I may find people  
(there)." \*The young man  
(then) departed, but he said to  
his uncle:—"I shall come  
again."

IV. \*After journeying a little,  
he came to a wigwam (where) a  
small boy came out (and) said:  
—"How is it with thine uncle?"  
<sup>b</sup>(The traveler) thought it  
strange:—"Can one so odd  
looking know all about our con-  
dition?" \*And he went on, and  
again he found a wigwam where  
there was a wizard, who at once  
saw that he (the traveler) was in  
trouble; that he looked sad.  
'Then the youth explained all  
to him. He described to him  
the terrible being. Immediately  
that man knew that this was  
Muttuntoe (the evil spirit). \*So  
he said to the young man:—"Do not think about it. I will  
overcome him. I will tell thee  
what thou shalt do, and I will  
explain to thee how to overcome  
him."

V. \* Withkeelno andah-wam-loohmoonda uhloomthoowh. Andah-nuhpahtah, wama wtilauch mookuhwaun wsheetul. \* Nul andah-keeshmeetthihteet, wtulwachpeen alningich keesha-wam-cheekhung neethkak. \* Wsheetul wtuhlaun nakah wtupeenang wauk wluqknuhaun wanpah-thauni alpookwuhk andauch pookwuheeng, warheetawshta nakah wsheetul wtupeenang. \* Nul wtilahmooltheen wtilkeeshich uhloowhweekwaun. \* Nul ninandpeethkak lawpee cheepawaun lawinda wcheerhakah-laun: "Ugh, dupih, neecheepah-waun konjawan; keeshajpe." \* Nul andah-tahwining kpuheekun, pajkcheewh withkeelno cheepenawqthoo uhj althith-poocheengwat uhpee. \* Wiyoh mawhaul linnapa weeshauth-oowh uhloomihlawh.

VI. \* Withkeelno wauk wsheetul nulowhwee ayahpoowhuk.

V. \* After the youth had been shown all, he departed. When he returned, the young man told all to his uncle. \* Then after they had eaten, ??? he swept up all the dirt. \* He put his uncle in his (the youth's) bed, and covered him with a white blanket with a peep-hole in it, and he lay down on his uncle's bed. \* Then he felt that something strengthened him (with power) to overcome. \* In the dead hour of night, the hideous monster again dropped down in the middle (of the wigwam). "Ugh!" (he said) "I am here. I am a monster. Be ready." \* Then when he opened the lid (of the basket bed), the young man, looking terrible, stepped out completely covered with feathers. \* That man-eater became frightened (and) departed (through the smoke-hole).

VI. \* The youth and his uncle are (still) living (there) contentedly.

#### PHILOLOGICAL COMMENTARY.

I. \* *Weekwaum* (A. \* *wigwôm*) 'house, dwelling' from  $\sqrt{\text{week}}$ . Cp. *Weekena* 'they dwell, inhabit' (A. *w'wiginô*), of which *weekwaum* is the cognate accus. :—'they inhabit a house.' Note the use of the present tense in narration to denote past relation. *Lawee* 'in the midst of' = O. D. *lawi* and A. *nôwi* (reduplicated *nânô-wiwi*) in the middle. See V. \* *Kohpe* 'forest' is undoubtedly

\* A. — Abenaki; O. D. stands for Old Delaware, the mixed language of the missionaries.

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cognate with A. *k'piwi* 'in the woods.' *Withkeelno* 'a young man,' composed of *withkee*, A. *uski*, Oj. *oshki* 'young' and *linno* 'man.' See on IV. <sup>4</sup>. *Wauk* 'and,' written *woak* in O. D. *Wsheetha* 'his uncle' = O. D. *schieess* 'uncle'; A. *nzāsīs* 'my mother-in-law's brother'; Oj. *nijishe* 'my uncle.' See I. <sup>b</sup>, <sup>1</sup>, but III. <sup>2</sup>, *wsheethul* with obviative *-l*. *Mahji* 'already' = O. D. *metschi* and A. *majimiwi* 'always'; cp. Oj. *aji* 'already.' *Kihkweelno* 'old man,' from *kihkwēe*; cp. O. D. *kikey* + *linno* 'man.' *Wrhalin* 'many'; cp. O. D. *chweli*. *Neeppnumo* 'summer' = O. D. *nipen*; A. *niben*; Oj. *nibin*.

I. <sup>b</sup> *Tah lickee* = O. D. *tah likhique* 'once upon a time.' Montour had written wrongly *tan lickee* here. O. D. *likhique* 'now, about this time.' *Weenamulthoo* (O. D. *winamallsin*, A. *akuamalsi*) 'he feels sick.' *Oonjeemawuh* 'he calls him'; cp. O. D. *wuntschiman* 'he summons him,' composed of *wuntshi* 'from' and *√ma* 'call'; so A. *uwikwimon* 'he calls him,' where the last part of the stem is identical with the Minsi. *Wlunquathitha* 'his nephew' = O. D. *lunk* 'nephew.' *Aleh-mawmjeenah-kihklolaut*. *Aleh* 'in order that'; *mawmjeenah* = O. D. *mamtschiisch* 'for the last time' (A. *mōmjessala*); *kihklolaut* is a reduplicated participle, 3 p. anim. 'he speaks' from *√klool*. See Prince, AJP., xxi, p. 298, on this stem and cp. A. *kalolōmuk* 'one speaks.'

I. <sup>a</sup> *Lawalindum*, cp. O. D. *uschuwelendam* 'he is grieved.' *Leetahah* 'he thinks' = O. D. *litchen*; A. *alidahōmuk* 'one thinks.' *Gutauch* for *ngutauch* 'I will make' (it), with *n-* pref. of 1 p. and *-ch* sign of the future (A. *-ji*). *Wlutshawha* 'so that it pleases him.' The first element is *wule-* 'good,' 'pleasing' (A. *wuli*). *Jeeth* 'my uncle' for *njeeth* = O. D. *nschieess*. Montour always leaves off the *n* prefix of the first person before a consonant; cp. below III. <sup>a</sup>; *dilnoom dulmeetheemich*.

I. <sup>a</sup> *Noolihtoomich* 'I will make it'; *n* = 'I'; 1 p. prefix; *oolihtoo* 'make'; *m* is the sign of inanimate; *ich* = fut. ending. Cp. A. *nolitonji* 'I will make it.' *Mihtqueenootee* = O. D. (Zeisberger) *michtquintotees* (dim.) 'a basket, something made of sticks'; cp. A. *w'mi* 'kwtonakwōnō' 'they pry it open with sticks.' *Kpuheekun* = O. D. *kpahikan* 'cover, lid'; 'something to shut'; cp. O. D.

<sup>1</sup> A. — Abenaki; O. D. stands for Old Delaware, the mixed language of the missionaries.

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more particularly with the position of Heider, as to the affinities of the brachiopods. The relationship between Phoronis, Bryozoa and Brachiopoda seems to me sufficiently close to justify the placing of them in the same phylum, though not in the same class, as Lang has done.

#### POSTSCRIPT.

Since this paper was written I have seen Ideka's (1901) very important contribution on the "Development, Structure and Metamorphosis of Actinotrocha." Ideka's work is in all respects the most thorough and extensive which has yet been done on the development of Actinotrocha, and in many very important points he differs decidedly from Masterman. Some of the differences between Actinotrocha and the brachiopod larva, which are pointed out on p. 65, disappear in the light of this work. For example, Ideka finds that there is but one complete septum in the body, that between the collar and the trunk, while the cavities of the preoral lobe and collar are in communication through a very incomplete septum. Furthermore Ideka finds no trace of a second pair of nephridia or of a "proboscis pore," such as Masterman described, while the two "chorda" diverticula of Masterman (Diplochorda) are represented by a single unpaired diverticulum in the Japanese species. Whether this is a glandular or skeletal structure is left an open question.

With the exception then of the single septum between the collar and the trunk regions there are no important differences between Actinotrocha and the brachiopod larva. This septum occupies a position in Actinotrocha corresponding to the posterior mantle furrow of the brachiopod larva, and it would be interesting to know whether, in stages of the brachiopod larva later than those which I have studied, any trace of a septum can be found in this position.

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ending. Cp. A. *wdi'lōn* 'he tells him.' *Ahwanitsh* 'someone' with *itsh* fut. ending. With *ahwani*, cp. O. D. *āuwen* 'who?' and 'someone'; also A. *awani*; Penob. *aweni*. *Pawhji* 'he will come.' Note that the fut. ending here is *-ji* as in A. Cp. O. D. *pejat* 'he who comes' and A. *wbaiōji* 'he will come.' See below *pawoich* the fut. participle. *Cheepeenawqthoo* 'one who looks strange,' from *cheepen* = O. D. *tschipin* 'strange' and *-awqthoo* 'he appears.' *Ahkōnjauptōona* 'one who is' (?) from *√kōnj* 'exist' (?). *Kweeshuloogkich* 'thou shalt fear it'; cp. O. D. *wischassin* 'he is afraid.' See below on II. <sup>4</sup>. *Shugk* 'but' = O. D. *shuk*. *Chee weeshuloogkōowih* 'fear thou not!' *Chee* = neg. prohibitive particle, as in IV. <sup>5</sup>. For *weeshul* see above. The neg. ending here is *-oowih*. *Muthkuneetahaul* 'be brave.' The stem *muthkun* is probably cogn. with Oj. *songi-* 'brave,' as in *songi-deewin* 'courage.' The Minsi ending *-eetahaul* undoubtedly contains the stem seen in *leetahah* 'he thinks'; cp. I. <sup>6</sup>, IV. <sup>6</sup>, and see on II. <sup>6</sup>. *Pawoich* 'he will come'; fut. participle *pawoit* + *ch*. See above *pawhji*. *Andah-laweetpihkahk* 'when it was midnight' = O. D. *lawitpikat*. It is a comb. of *lawi* 'midst' and *pihkahk* 'night'; cp. A. *nōwitebakak* 'midnight.' *Andah-wam-quack-kawet*. *Andah* 'when'; *quack* 'thing'; also 'what?' (cp. O. D. *keco*? A. *kagui*?). It should be written *queq* and not *quack*. *Kawet*, ptc. 3 p. 'it, he sleeps'; cp. A. *kawi*; Oj. *nin gawingwash* 'I fall into a deep sleep' For this whole sentence, cp. A. :—*lōni adoji msiwi kagui kawit* (in A. we usually find the recipr. form as *kawold'wak* 'they are asleep').

II. <sup>6</sup> *Nulnuh*; see on I. <sup>6</sup>. *Peethkahkeek* 'it was night'; cp. O. D. *pisgeu* 'dark'; *pisgeep* 'it was night' (*-eep* = sign of the past); cp. A. *pesgid'bakak* 'it is dark.' *Mahji* 'already'; see on I. <sup>6</sup>. *Keeshmeettheeteetah* 'they had eaten'; ptc. 3 p. pl. *Keesh* = sign of perfect; *meetthee* 'eat' + *teet*, ending of 3 p. pl. ptc.; *ah* = temporal ending as in *waupungeeka*, I. <sup>6</sup>. In A. *kisi-mitsihidit* 'after they had eaten'; cp. O. D. *mixin* 'one eats' and *mizewagan* and *mitsuwagan* 'food' (the last form from Zeisberger). Montour renders here freely 'after the evening meal,' but this would necessitate the use of the word *ulakunipoagan* 'supper.' *Awuthee* 'opposite.' *Tindawing*, loc. 'at the fire,' from *tindey* 'fire.' *Lmutawpoowh* 'he sat'; cp. O. D. *wulumachdappin* 'he

<sup>5</sup> Note that *j* in O. D. has the value of consonantal *y*.



sits with his legs in front of him'—*i. e.*, on the ground. The last part of this combination contains the same root as that seen in *ahpeerwuyuhpeen* (I.) 'bed' and A. *abi* 'sit.' *Pahtoon* 'he waits'; cp. O. D. *pehawah*, *pehowen* 'he waits.' *Tah* 'how,' the same element seen in *taunha*, IV. <sup>a</sup>. *Nij* 'that' with fut. sign. *Alak* 'which is'; *al* = rel. particle + *ak* 3 p. ptc. ending inan. *Nih aleet* 'that which is'; cp. I. <sup>a</sup> and *laweetpihkahk*, I. <sup>a</sup>.

II. <sup>b</sup> *Weerhkawa* 'suddenly'; cp. O. D. *wiechgawotschi* 'unexpectedly.' *Quack konjwah wuhkoong* 'something there was above.' With *wuhkoong* cp. O. D. *hokunk*, probably cogn. with A. *agudar* 'above.' *Ahwan*, see on I. <sup>b</sup>; *cheepenawqthoo*, see on I. <sup>b</sup>. *Wcherhakahlaun* 'he jumps down' = O. D. *loaktschehellen*. *Keerhkee th'q'ta* 'by the fire.' With *keerhkee* cp. O. D. *giechgi* 'near, by' and with *th'q'ta* 'fire' cp. A. *skweda*; Passa. *skwut*; Oj. *ishkote*. This seems to be a pure Minsi expression. *Tindey* is the Unami word; see II. <sup>a</sup>.

II. <sup>c</sup> *Owh* 'he said'; cp. Oj. *iwa* 'he says.' *Baum* 'here, hither'; see also II. <sup>a</sup>. Is this cogn. with Oj. *oma* 'here'? *Konjahwan* 'I am'; partic. 1 p. sg. See below on II. <sup>a</sup>. *Nhukee*, lit. 'my body' = 'I myself'; cp. III. <sup>a</sup>, *whukee* 'himself.' In O. D. *hakey* is 'body'; cp. A. *nhaga* 'my body,' but it is not used to denote the emphatic pronoun. In Oj., however, we find *niaw* 'myself'; lit. 'my body.' The A. pronoun *nia* 'I' may be cogn. with this. *Nmihwa* 'I eat'; cp. A. *n'môwô* 'I eat him.' In A. *mitsi* = 'eat' in general, as 'a meal,' but *môwô* means rather 'devour.' *Linno* 'man,' the same stem contained in *lenâpe* 'a male creature'; see Prince AJP., xxi, p. 298 n. 1. *Ktuhaulaw* 'thou lovest him'; *naulaw* (we expect rather *ntuhaulaw*!) 'I want him' = O. D. *ahoalan* 'love'; cp. Prince, *op. cit.*, p. 299. *Kweeshathee* 'thou fearest me.' Note ending of 1 p. -*ee*.

II. <sup>d</sup> *Mutahkawah* 'he fought with' = O. D. *machtagen*, perhaps cogn. with A. *miga'kamuk* 'one fights.' *Wcelno* (?) 'wild animals'; so Montour, but I cannot find the stem. *Wun* demonstr. 'that'; cp. A. *wa*. *Keemoorh* 'wizard,' probably = O. D. *kemochwen* 'one who steals away something secretly.' *Konjahwan* partic. 3 p. 'as he was'; see above II. <sup>c</sup>. *Weeshulooko* 'he scares him.' See above on I. <sup>b</sup>, II. <sup>c</sup>. *Nawkawh* = O. D. *nakewi* 'a little while'; cp. A. *n'makaiwi*.

II. <sup>e</sup> *Nul* is used as a resumptive exactly like Passa. *nit*, which occurs so often at the beginning of a sentence. It is a demonstra-

tive originally. Cp. *nulhuhnuh* I. <sup>1</sup>, and *nulnuh* II. <sup>2</sup>. *Muthkuncetahah* 'summoning his courage.' See on I. <sup>2</sup>. It has the temporal ending here *-ah*, as in *waupungeeka* I. <sup>2</sup>. *Neepahwoowh* 'he stood erect' = O. D. *nipackton*. *Mawhah* 'not'; cp. O. D. *matta* 'not.' *Geesh* 'I can' for *ngeesh*. *Keeshajpinahwa* with neg. ending *-wa* (cp. IV. <sup>2</sup> and I. <sup>2</sup>) from *keeshajpin* 'be ready'; cp. O. D. *gischhatton* 'be ready,' also the form *keeshajpinawitch*, 3 p. inv., 'let him be ready.' A. has *kizôjo* 'he is ready.' *Yohquh* 'now again' = O. D. *yucke*, used as a sort of resumptive. *Lawpeewhich*, a comb. of *lawpee* 'again' and *peewhich* 'I shall come' (for *npee-which*); cp. III. <sup>2</sup>. *Baum* 'hither'; see II. <sup>2</sup>.

II. <sup>1</sup> *Ktiithpihlaun* 'he jumps up'; cp. *wcherhakahlaun* 'he jumps down,' II. <sup>2</sup>, and *uhloomihlawh* 'he goes up,' V. <sup>1</sup>. The ending *-ihlawh* seems to mean 'jump.' *Aleenqahtang* (loc. *-ang*) 'through the smoke-hole.' It is probably connected with O. D. *linquechin* 'look.'

III. <sup>2</sup> *Lmutahpoowh*, see on II. <sup>2</sup>. *Lawpeewh* 'again' = O. D. *lappi*. See on II. <sup>2</sup> *lawpeewhich*. *Wtilawul*, see on I. <sup>2</sup>. *Whukee*, see on II. <sup>2</sup>. *Yul*, pl. of *yun* (inan.); cp. A. *yûlil* 'these,' pl. of *yû* 'this' (inan.).

III. <sup>2</sup> *Kalahaat* 'truly' is a comb. of *kalah* = O. D. *kehella* 'verily, yes'; Penob. *kehela*, and *aat* the ptc. of 'to be.' The literal translation is 'true it is.' A. *kalaato* 'verily' is an exact equivalent of *kalahaat*. *Cheepahwan* 'one who looks horrible'; cp. O. D. *tshipilen* 'it is awful.' See V. <sup>2</sup>. *Shurhke* 'certainly' = O. D. *schachachki* 'surely.' *Nickuloogki-ch* 'he will leave me,' from  $\sqrt{\text{nickul}}$  = O. D. *nukalan* 'forsake' + *i-*, ending of the 1 p. as in *kweeshathee*, II. <sup>2</sup>. For *jeeth*, see I. <sup>2</sup>. *Quackwich-ha*; *quack* with fut. ending + the particle *-ha* (see on I. <sup>2</sup>). The *w*-ending in *quackwich* shows that this word must really be pronounced *quackw* (so Anthony in *Len. Dict.*; *queq* under *kolku*). *Dilnoom* 'I do it' for *ndilnoom* (?). *Dulmeetheemich* 'I will go,' for *ndul-*, from *aal* (see *Len. Dict.*, under  $\sqrt{\text{aan}}$  'go'). The past of this verb is *ahloomthoowh* 'he went,' III. <sup>2</sup>, V. <sup>2</sup>. *Ahlih-wthihkawh*; *ahlih*, rel. particle as A. *ali* 'where' + *wthihkawh* with loc. ending *-k* = O. D. *wsigau* 'sunset.' *Tauthrha* 'I (shall) find' (?). *Ahwanah* 'people,' really 'someone,' from *ahwan* (see on I. <sup>2</sup>).

III. <sup>2</sup> *Wsheethul* 'his uncle' is obviative with characteristic ending *-ul*. In I. <sup>2</sup>, <sup>2</sup> and <sup>1</sup>, Montour has written *wsheetha* (?).

IV. <sup>a</sup> *Aloorhwa* 'he traveling,' participle; cp. O. D. *miss-ochwen* 'he walks about.' *Quack* must mean 'somewhat.' *Yih*, dem. pron., probably 'a certain.' *Thkuhinthoowh* 'a small boy' = O. D. and Unami *skahenso* (see *Len. Dict.*, p. 115). *Patchih-kheewh* 'there came forth,' from O. D. *ktschin* 'go out'; see on V. <sup>1</sup>. *Taunha wtindin* = A. *tôni wdain* 'how is he?' *Ksheeth* see II. <sup>c</sup>.

IV. <sup>b</sup> *Mawshalindum* and *mawsheelawahkoo* appear to be alternative synonyms. The first is written in parentheses in Montour's MS. *Almawsheel* probably means 'that (*al* = rel. particle) one so strange.' *Wam* 'all'; see I. <sup>a</sup>. *Wawihtoon* 'he knows it' (inan.); cp. A. *n'wawawinôwô* 'I know him.' *Aylackwloowheen* 'our condition'; *aylack* = O. D. *elek* 'as it is'; *wloowheen* 'our being thus.' I have translated it in the 3 p. for the sake of the English.

IV. <sup>c</sup> *Lawpeewh* 'again'; see on II. <sup>a</sup> and III. <sup>a</sup>. *Moorhkum* 'he found' = O. D. *mochgamen*. *Ahwawhlihkoo* probably 'there was a wizard' (so Montour). *Shawa* = O. D. *schawi* 'at once'; occurs also IV. <sup>d</sup>. *Wninahko* 'he knows'; cp. *wninootumin*, IV. <sup>d</sup>, and Prince, *op. cit.*, p. 298. *Wtil-sheewalindumoo* 'he feels sad'; *wtil*, pref. 3 p. (A. *wdelli*); *sheewa* 'sad' (O. D. *schiwamallsin* 'he feels grieved'); *lindumoo*, the ending denoting a state of mind; cp. I. <sup>a</sup>, <sup>c</sup>. *Weenawqthowh* 'he looks sad,' from *ween*, same stem as in *weenamulthoo*, I. <sup>b</sup>, + *awqthowh* 'he looks,' as in *cheepeen-awqthoo*, I. <sup>a</sup>; II. <sup>b</sup>.

IV. <sup>d</sup> *Wam*, see I. <sup>a</sup>; IV. <sup>b</sup>. *Wtilauch* seems to be a fut. 'he will tell him'; see also in V. <sup>a</sup>. It is probably used here vividly. *Mookuhwaun* appears to be a synonym of *withkeelno* 'youth.' *Wtil-wturhquon* 'he describes to him,' from *wtil*, pref. 3 p. +  $\sqrt{wturh}$  + *quon*, ending 3 p. sing. (see Prince, *op. cit.*, p. 298). *Wninootumin*, 3 p. sing. inan. with def. *-in*, as in A. *n'wajônem awikhigan* 'I have a book,' but *n'wajônemen awikhigan* 'I have the book.' *Wuh linno* 'that man.' With *wuh*, cp. A. *wa* 'that.' *Nunrhat* is probably a participial formation as shown by *-at*. *Muttontoe* must be connected with O. D. *mattonheen* 'he curses' and *-to*, the same ending seen in *Manitto* 'Spirit.' It is clearly a cognitive of A. *madahôdo* 'evil spirit.'

IV. <sup>e</sup> *Chee quack leetakhawa* 'don't think anything about it,' not translated at all by Montour. Composed of *chee*, prohib. 'dонт' (cp. I. <sup>b</sup>) + *quack* 'anything' + *leetahah* 'think' (occurs also

I. <sup>b</sup>). Note the neg. ending *-wa*, as in II. <sup>a</sup>. *Dulwihkawawh* (for *ndul-*) 'I will overcome him'; cp. *ahloowhweekahwut* 'the way to overcome him.' The stem is seen in O. D. *allowat* 'strong, mighty.' *Ktihi* 'I tell thee'; cp. A. *kdi'lel*, both from  $\sqrt{il}$ . *Yoonich* = *yoon* 'this' + *ich* (fut.) used here as relative 'what.' *Ktilnumin* 'thou shalt do it'; see III. <sup>b</sup>. *Wauk ktiloohmoolin* 'and I will explain it to thee.' The *k-* prefix = 'thee'; the ending *-ool* = 1 p. 'I' + the def. *-in*. See Prince, *op. cit.*, p. 299. *Wanjich* = O. D. *wentschi* 'for, in order that' with fut. *-ch*.

V. <sup>a</sup> *Andah wam loohmoonda* 'when he had shown him all' (not translated correctly by Montour); from O. D. *allohumassin* 'he shows it.' *Uhloomthoowh* 'he departed'; also III. <sup>b</sup>, <sup>a</sup>; IV. <sup>a</sup>. Note the lack of subjects here which must be supplied by the context. I have avoided this by a passive periphrasis. With *nupah-tah* 'return,' cp. O. D. *apatschin*.

V. <sup>b</sup> *Andah keeshmeetthihsteet*, so in II. <sup>a</sup>. *Wtulwachpeen alningich* I cannot translate. Montour's MS. is confused at this point. *Keesha*, sign of perfect, as *geesh* in II. <sup>a</sup>; *wam* 'all'; *cheekhung*, from same stem as O. D. *tschikhammen* 'he sweeps it.' *Neethkak* 'dirt' = O. D. *niskeu*. The last part of this stem *-eethk*, O. D. *isk* seems to be cogn. with Oj. *aj-ishki* 'mud.'

V. <sup>c</sup> *Nakah wtupeenang* 'on his bed'; *nakah* 'on'; *wtupeenang* from *ahpee* 'bed' (cp. I. <sup>a</sup>) with pref. 3 p. *w* with infixed *t* before a vowel. *Wlugknuhaun* 'he covers him'; cp. O. D. *mettack-quohemen* 'he covers it' and Oj. *pada-gwanawa*; the common stem evidently being  $\sqrt{kwena}$ . *Waupahthauni* = O. D. *woapach-saney* 'white blanket.' *Alpookwuhk andauch pookwuheeng*, lit. 'he made a hole there in a hole'; cp. O. D. *pquihillen*. *Andauch* = *undach*. *Warheetawshhta*, probably 'he lies down.'

V. <sup>d</sup> *Wtilamooltheen* 'he feels'; with *-mooltheen*, cp. I. <sup>b</sup>. *Wtil-keeshich* 'he will make him'; cp. O. D. *gisch* 'make'—i. e., 'he feels someone making him (giving him power) to overcome.' *Uhlowhweekwaun*; cp. IV. <sup>a</sup>.

V. <sup>e</sup> *Nin andpeethkakh*, see on II. <sup>a</sup>. *Lawinda* 'in the midst'; cp. I. <sup>a</sup>. *Dupih* 'I am (here)' from *uhpee* = O. D. *achpin* 'be in a place'; A. *abi* 'sit.' *Keeshajpe* 'be ready' (inv.), see on II. <sup>a</sup>.

V. <sup>f</sup> *Andah-tahwining* 'when he opened' = O. D. *tauwunnum-men* 'he opens it.' *Kpuheekun*, see on I. <sup>a</sup>. *Pajkcheewh* 'there

came forth'; cp. *patchihkcheewh*, IV. \*. *Uhj* (?). *Althithpoocheengwat uhpee* 'he is covered with feathers'; see I. \* *uhpeeyuhk*.

V. \* *Wiyoh*, demonstr. pron. *Mawhaul linnapa* 'he who eats man'; cp. *n'mikwa* 'I devour,' II. \*. On *linnapa* from *linno* 'man' and *-ape* 'a male' *par excellence*; the race name of the Delawares, see Prince, *op. cit.*, 295, n. 1. *Weeshauthoowh*, see I. \*; II. \*. *Uhloomihlawh* 'he jumped up'; cp. *ktithpihlaun*, II. '.

VI. \* *Nulowhee* 'well, happily.' *Ayahpooowhuk* 'they dwell' from  $\sqrt{ahp}$ ; A. *abi* 'sit.'

*Stated Meeting, January 17, 1902.*

President WISTAR in the Chair.

Present, 11 members.

General Wistar, in taking the Chair, returned thanks for the honor done him in election to the Presidency of the Society, and offered some remarks concerning the future welfare of the Society.

The list of donations to the Library was laid on the table, and thanks were ordered for them.

The decease of the following members was announced :

Cornelius Petrus Tiele, Ph.D., D.C.L., at Leyden, on January 11, 1902, aged 71 years.

Philip P. Sharples, at West Chester, Pa., on January 15, 1902, aged 91.

Prof. Alpheus Hyatt, at Cambridge, Mass., on January 15, 1902, aged 63.

The Standing Committees for the ensuing year were chosen, as follows :

*Finance*.—Philip C. Garrett, William V. McKean, Joel Cook.

*Hall*.—Joseph M. Wilson, Harold Goodwin, John Marshall.

*Publication*.—Henry Carey Baird, Patterson DuBois, Joseph Willcox, Amos P. Brown, William H. Furness, 3d.

*Library*.—George F. Barker, Albert H. Smyth, J. G. Rosengarten, Edwin G. Conklin, R. C. H. Brock.

The meeting was adjourned by the presiding officer.

*Stated Meeting, February 7, 1902.*

President WISTAR in the Chair.

Present, 10 members.

Hon. James T. Mitchell, on behalf of the Committee on Historical Documents, reported that arrangements had been made for the publication in full of the original journals of Lewis and Clark.

The following were elected officers to fill vacancies :

*Vice-President*, Prof. Samuel P. Langley.

*Councilor*, Prof. Ira Remson.

The Society was adjourned by the President.

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*Stated Meeting, February 21, 1902.*

Mr. BENJAMIN SMITH LYMAN in the Chair.

Present, 3 members.

Letters were read from Prof. Samuel P. Langley, acknowledging his election to the Vice-Presidency, and from President Ira Remson acknowledging his election as a Councilor. A communication was received from the Congrès International des Orientalistes de Hanoï, announcing the opening of an International Exposition, and of a Congress of Orientalists in connection with it, at Hanoï in November next, and asking the Society's coopération.

The list of donations to the Library was laid on the table, and thanks were ordered for them.

The meeting was adjourned by the presiding member.

*Stated Meeting, March 7, 1902.*

President WISTAR in the Chair.

Present, 25 members.

A letter was received from the Committee formed to arrange for the XIII International Congress of Orientalists, to be opened at Hamburg, on September 4, 1902, inviting this Society to send a special delegate to the Congress, and on motion the President was authorized to appoint a delegate to represent the Society.

The list of donations to the Library was laid on the table, and thanks were ordered for them.

The decease was announced at Philadelphia, on March 2, of Francis W. Lewis, M.D., aged 76 years.

The meeting was adjourned by the President.

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*Stated Meeting, March 21, 1902.*

President WISTAR in the Chair.

Present, 9 members.

A letter was read from the Secretary of the Nobel Committees of the Royal Academy of Science at Stockholm, enclosing the Code of Statutes of the Nobel Foundation.

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*General Meeting, April 3, 4 and 5, 1902.*

Present, 115 members.

APRIL 3.—MORNING SESSION, 10 A.M.

President WISTAR in the Chair.

The President delivered an Address of Welcome.

The Secretaries presented a communication from the Ad-

visory Committee in Astronomy of the Carnegie Institution (Prof. E. C. Pickering, Chairman), inviting suggestions regarding investigations in astronomy, which should be aided by the Carnegie Institution.

The following papers were read :

"Origin of the Oligocene and Miocene Deposits of the Great Plains," by Prof. John B. Hatcher, of Pittsburg.

"The Upper Cretaceous and Lower Tertiary Section of Central Montana," by Prof. W. B. Scott, for Mr. Earl Douglass, of Princeton.

"On South American Mammals," by Prof. William B. Scott, of Princeton.

"The Mammals of Pennsylvania and New Jersey," by Mr. Samuel N. Rhoads, of Audubon, N. J.

"The Identity of the Whalebone Whales of the Western North Atlantic," by Dr. Frederick W. True, of Washington.

#### AFTERNOON SESSION, 2 P.M.

President WISTAR in the Chair.

The following papers were read :

"On the Molluscan Fauna of the Patagonian Formation," by Prof. W. B. Scott, for Dr. H. von Ihering, of São Paulo, Brazil.

"A Comparison between the Ancient and Recent Molluscan Fauna of New England," by Prof. Edward S. Morse, of Salem, Mass.

"Distribution of Fresh-water Decapods and its bearing upon Ancient Geography," by Prof. Arnold E. Ortmann, Ph.D., of Princeton.

"Systematic Geography," by Prof. William Morris Davis, of Cambridge, Mass.

"On Drift Casks in the Arctic Ocean," by Mr. Henry G. Bryant, of Philadelphia.

"On the Magnetic Properties of Nickel," by Mr. Joseph Wharton, of Philadelphia.



## EVENING SESSION, 8 P.M.

The following papers were read :

" The Relation of the American University to Science,"  
by President Henry S. Pritchett, of Boston.

" The Advancement of Knowledge by the Aid of the  
Carnegie Institution," by President Daniel C. Gilman, of  
Baltimore.

## APRIL 4.—MORNING SESSION, 10 A.M.

Vice-President LANGLEY in the Chair.

The following papers were read :

" Results of Observations with the Zenith Telescope at  
the Sayre Observatory," by Prof. Charles L. Doolittle, of  
Philadelphia.

" On a New Method of Transiting Stars," by Prof.  
Monroe B. Snyder, of Philadelphia.

" On the Evolution of Martian Topography," by Mr.  
Percival Lowell, of Flagstaff, Ariz.

" Historical Investigation of the Supposed Changes in the  
Color of Sirius since the Epoch of the Greeks and Romans,"  
by T. J. J. See, Ph.D., of Washington.

" Recent Progress in the Lunar Theory," by Prof. Ernest  
W. Brown, F.R.S., of Haverford, Pa.

" On the Spectra of Gases at High Temperature," by Prof.  
John Trowbridge, of Cambridge, Mass.

## EXECUTIVE SESSION, 12.40 P.M.

President WISTAR in the Chair.

Pending nominations were read, and the candidates for  
membership were balloted for, and the Secretaries reported  
the election of the following :

Residents of the United States—

John A. Brashear, Sc.D., Allegheny, Pa.

Andrew Carnegie, LL.D., New York.  
Prof. William B. Clark, Baltimore.  
Prof. Hermann Collitz, Ph.D., Bryn Mawr.  
Grove K. Gilbert, Washington.  
President Arthur Twining Hadley, New Haven.  
Prof. George E. Hale, Williams Bay, Wis.  
Prof. Paul Haupt, Baltimore.  
Prof. Albert Abraham Michelson, Sc.D. (Cantab), Chicago.  
C. Hart Merriam, Washington.  
Prof. Theodore William Richards, Cambridge, Mass.  
Prof. Felix E. Schelling, Ph.D., Philadelphia.  
Prof. Robert Henry Thurston, Ithaca.  
Benjamin Chew Tilghman, Philadelphia.  
Prof. Robert S. Woodward, New York.  
Foreign Residents—  
Antoine-Henri Becquerel, Paris, France.  
Jean-Gaston Darboux, Paris, France.  
Sir Michael Foster, F.R.S., D.C.L., Cambridge, Eng.  
Prof. G. Johnstone Stoney, F.R.S., London, Eng.  
Prof. Silvanus P. Thompson, F.R.S., London, Eng.

#### AFTERNOON SESSION, 2 P.M.

President WISTAR in the Chair.

The following papers were read :

"Is Scientific Naturalism Fatalism? A one-minute paper" by Prof. William Keith Brooks, of Baltimore.

"On Dichotoma, a New Genus of Hydroid Jelly-Fish," by Prof. William Keith Brooks, of Baltimore.

"On Some Equations Pertaining to the Propagation of Heat in an Infinite Medium," by Prof. A. Stanley Mackenzie, of Bryn Mawr, Pa.

"On the Law of Magnetic Hysteresis," by Prof. M. I. Pupin, of New York.

"On the Continuity of Protoplasm," by Prof. Henry Kraemer, of Philadelphia.

"The Embryology of a Brachiopod," by Prof. Edwin Grant Conklin, of Philadelphia.

"Relationship of the Gordiacea," by Prof. Thomas H. Montgomery, Jr., of Philadelphia.

"The Spermatogenesis of *Oniscus Asellus*, Linn., with Especial Reference to the History of the Chromatin," by Prof. E. G. Conklin, for M. Louise Nichols, Ph.D., of Philadelphia.

"The International Catalogue of Scientific Literature," by Cyrus Adler, Ph.D., of Washington.

#### APRIL 5.—MORNING SESSION, 10 A.M.

Vice-President SELLERS in the Chair.

The following papers were presented:

"Experiments on Cytolysis," by Prof. Simon Flexner, of Philadelphia.

"A Classification of Economies," by Prof. Lindley Miller Keasbey, of Bryn Mawr, Pa.

"On Osteitis Deformans," by Prof. James C. Wilson, of Philadelphia.

"The Influence of Acute Alcoholic Intoxication upon Certain Factors Involved in the Phenomena of Hæmotolysis and Bacteriolysis," by Prof. A. C. Abbott, of Philadelphia.

"Blindness from Congenital Malformation of the Skull," by Charles A. Oliver, M.D., of Philadelphia.

"The Isthmian Canals," by Prof. Lewis M. Haupt, of Philadelphia.

"Race Elements in American Civilization (illustrated by German Examples)," by Prof. M. D. Learned, of Philadelphia.

THE EMBRYOLOGY OF A BRACHIOPOD,  
TEREBRATULINA SEPTENTRIONALIS Couthouy.

EDWIN G. CONKLIN, PH.D.

(FROM THE ZOOLOGICAL LABORATORY OF THE UNIVERSITY OF PENNSYLVANIA.)

Plates I-X.

(Read April 4, 1902.)

I. INTRODUCTION.

1. *Historical.* — Although Brachiopoda are chiefly notable because of their great abundance in past geological periods, their relationships to other groups of animals are still so obscure as to make them objects of great interest to the general morphologist. At different times and by different investigators they have been variously regarded as allied to Mollusca, Polyzoa, Annelida, Chætogonatha and Phoronis, while others have regarded them as a distinct phylum of the animal kingdom. Even at the present time there is no uniformly accepted view as to their relationships, all of the above affinities (excepting possibly the first) being maintained by different authors. Of the two morphological methods of investigating relationships, viz., Comparative Anatomy and Comparative Embryology, the former has been applied to this group of animals in a number of noteworthy cases. Not to mention the large number of older and less important works on this group, the comprehensive studies of Albany Hancock ('58) and the excellent researches of Lacaze-Duthiers ('61), which are still models of accuracy, the extended labors of Davidson ('86-'88) and most recently the series of splendid contributions by Blochmann ('92 and 1900) have made us as well acquainted with the anatomy of the brachiopods as we are with the anatomy of most other invertebrates.

The case stands far differently with the embryology of this group. But two writers have as yet attempted to deal with the entire embryology of a brachiopod, and both of these studies were made without the employment of serial sections or modern microscopical and micro-technical aids.

Neglecting the isolated observations of Fritz Müller ('60 and '61) of a free-swimming larval brachiopod, and the more extended but still very fragmentary observations of Lacaze-Duthiers ('61) on the development of *Thecidium*, the credit of having made the first study of the entire development of a brachiopod belongs to the

American naturalist, Prof. E. S. Morse ('71-'73). How thorough and complete this work was I shall have occasion to remark in the further course of this paper; but done as it was at a time before good microtomes and imbedding means were invented, and long before serial sections were thought of, it could not but leave much of the internal structure of the embryo undetermined, especially as the eggs and embryos of the form studied (*Terebratulina septentrionalis*) are quite small and opaque. Nevertheless Morse's work stands to-day as one of the two most important works on the embryology of the brachiopods. The other work referred to is the later but more detailed and comparative "Observations on the Development of Brachiopods," by the great Russian zoölogist, Alexander Kowalevsky (1874). Kowalevsky's work, which was published in Russian, remained practically unknown to those not acquainted with that tongue until 1883, when Oehlert and Deniker published an excellent abstract of it. In this work Kowalevsky describes his observations on the development of four species—*Argiope* (*Cistella*) *neapolitana*, *Thecidium mediterraneum*, *Terebratula minor* and *Terebratulina caput-serpentis*; only a few observations were made on the development of the two last-mentioned species, but his work on *Cistella* and *Thecidium* was detailed in character and nearly complete so far as the stages of development are concerned. Although Kowalevsky employed isolated sections to a limited extent in his work and also shows certain details of internal structure in many figures of entire embryos, yet his work of necessity left many important problems of structure unsolved.

In 1879 Prof. W. K. Brooks discovered the free-swimming larvæ of *Lingula* (*Glottidia*) *pyramidata* and described in detail the structure and further development of these larvæ up to the adult condition. This work, although dealing only with the larval stages and metamorphosis, is still the most complete extant on the development of the Ecardines, the most primitive group of the brachiopods. With characteristic insight Brooks has used his many important discoveries on the later development of *Glottidia* in an extremely valuable discussion of the systematic position of the brachiopods.

The small portion of Shipley's (1883) paper on *Argiope* (*Cistella*) which treats of the development of that form adds little to the much more extensive work of Kowalevsky on that animal. His principal contribution consists in his determination of the fact that

the so-called "segments" of the larva are not true segments, as Kowalevsky supposed, but are mere folds in the body wall.

The papers by Beecher ('91, '92, '93) on the development of brachiopods deal almost entirely with the developmental changes which occur in the shell and not with the general embryology. Beecher has proposed a very interesting and important classification of the brachiopods based on the developmental characters of the shell; since however the present work deals only with the early embryology, we need not further consider Beecher's work here.

2. *Material*.—For the material which has formed the basis of this study I desire at the outset to express my profound obligations to my friend Dr. Edward G. Gardiner, of Wood's Holl, Mass. Dr. Gardiner had collected the material (which consists of about thirty different stages in the early embryology of *Terebratulina septentrionalis*, forming a fairly complete series from the unsegmented egg up to the beginning of the metamorphosis) at Eastport, Me., during the early summer of 1894. For various reasons he was prevented from making an immediate study of this material, and when in the summer of 1898 in conversation with him I expressed my desire to study the cell lineage of a brachiopod, he graciously offered me the material which he had collected with the request that I should use it in any way I might see fit. I soon found that it would be impossible to work out the cell lineage, not only because of a lack of sufficient number of cleavage stages, but also and chiefly because of the great difficulties which the material itself offered; the eggs were quite opaque and, except in a few cases, it was impossible to render the nuclei visible in preparations of the entire egg; the cleavage was almost entirely equal and I was unable to find any constant landmarks which might be used in orientation, and finally the cleavage was found to be more or less irregular and inconstant. I was compelled therefore to abandon the plan to study the cell lineage of *Terebratulina* and the material was laid aside, until a few months ago I found opportunity to again take up this subject with the view of working out the early development of this interesting animal in as great detail as the material would allow.

3. *Methods*.—All the material was, I believe, preserved in Perenyi's fluid, and while the general form and size of the embryo as a whole, and also of its constituent cells and nuclei, has been faithfully preserved, every trace of the cilia, which according to Morse ('71-'73) cover the surface and line the alimentary tract and

body cavity, has entirely disappeared. The method of fixation, together with the long residence of the material in alcohol, rendered it difficult to stain. The picro-hæmatoxylin, which I have used with such good results in other cases, was of little value here, and I have found that in the preparation of entire eggs or embryos the most useful stain is borax carmine, while in the preparation of sections iron hæmatoxylin has given the best results. Both entire preparations and serial sections were mounted in balsam and studied and drawn under an immersion lens (Zeiss. Apochromat. 3 mm., Comp. Occ. 4).

Perhaps I may be pardoned a word in defense of the rather large use of surface views and optical sections which I have made in this paper. This has not been due to the fact that I have made few serial sections, for I have made and studied serial sections of many hundreds of embryos, but because with material which is at all favorable the orientation of the embryo and the interrelation of its various parts can be more safely and satisfactorily determined from the study of whole embryos than by means of serial sections; and this is especially true where it is possible to use an immersion lens in the study of entire preparations. Further, more points of structure can be shown in a single figure of this kind than in dozens of figures of serial sections. Of course, serial sections must always be used in connection with the study of entire preparations, and in the present paper all the details of internal structure which are shown in the surface views and optical sections have been confirmed again and again by serial sections. Any one accustomed to the study of both entire preparations and serial sections knows that few things are more deceptive than the latter when not checked by a study of the former, while the publication of whole series of sections contributes more to the pride of the author and the income of the illustrator than to the edification of the reader.

## II. THE EGG AND ITS CLEAVAGE.

Morse ('71) has described the method of egg laying, and has called attention to the fact that the mature eggs are usually kidney-shaped, though they vary considerably in shape and size. None of the unsegmented eggs which I have examined are kidney-shaped; they are slightly elliptical, being about  $160\ \mu$  in the longest diameter and  $144\ \mu$  in the shortest. This elongation of the egg in one

axis is probably the precursor of the first cleavage at right angles to that axis. Morse ('73) also mentions the presence of a "distinct granular membrane, the ovishell, which is formed while the eggs are still in the perivisceral cavity." I have found this membrane in all early stages (Figs. 1-10), though I have not been able to recognize it after about the twenty-cell stage. From the fact that it lies close to the periphery of each cell, following all of its individual curvatures (Figs. 2-10), I am convinced that it is not a distinct membrane but only a peripheral layer of clear protoplasm (ectoplasmic layer of Harmer). There is no protoplasmic area in the egg distinct from the yolk, though there is a slight aggregation of protoplasm around the nuclei, but the entire egg is densely packed with small yolk granules which render it opaque.

I have not attempted to study the nuclear phenomena of the maturation and cleavage since the material is very unfavorable for such work. Two polar bodies are formed, the first of which soon after divides (Figs. 1 and 2). These polar bodies do not remain attached to the egg after the sixteen-cell stage, and in some eggs they appear to pass into the cleavage cavity, though in such cases it is difficult to distinguish between polar bodies and small spherules which are cut off from the inner ends of the cleavage cells, and which contain protoplasm and yolk but no nuclei (Figs. 11 and 37). At the stage when the gastrulation begins these spherules are found in considerable numbers in the cleavage cavity (Fig. 37); they disappear in later stages. Similar spherules have been observed by Caldwell ('85) in *Phoronis*.<sup>1</sup>

The first cleavage is meridional and divides the egg into two slightly unequal blastomeres (Fig. 2); the second cleavage is also approximately meridional and divides each of the blastomeres equally; as a result of this cleavage four blastomeres are formed, two of which are somewhat smaller than the other two (Fig. 4). A polar furrow is present (Figs. 4 and 7) which, taken in connection with the overlapping of certain cells (Fig. 3), indicates that in some eggs at least the cleavage is of a spiral type. The third cleavage is equatorial and leads to the formation of eight blastomeres, all of which are nearly equal in size (Figs. 5, 6, 7); in some eggs the four cells at the animal pole lie just above those at the vegetal pole (Fig. 6); in others they have rotated through various

<sup>1</sup> Quite recently Ideka (1901) has fully described these spherules in *Phoronis*; he calls them *plasmic corpuscles*.



angles (Figs. 5 and 7). In the eight-cell stage a considerable cleavage cavity appears with openings at the animal and vegetal poles (Figs. 6 and 7).

The cleavage forms just described and represented in Figs. 1-7 are among the most regular ones observed; others are irregular and unequal from the first. One of the most common variations is produced by very unequal divisions, the chief mass of the egg seeming to bud off small cells, usually at the animal pole (Fig. 8). Later stages in which one or two of the blastomeres are much larger than the others, and in which the cleavage cavity is smaller than usual, are not infrequently found. Such eggs appear to give rise to normal blastulæ, in which all the cells are of equal size, by the more rapid division of these larger blastomeres.

The eight-cell stage gives rise to the sixteen-cell stage by the meridional division of each of its blastomeres. Fig. 7 shows each blastomere of the eight-cell stage indented at its periphery, preparatory to this division, which occurs simultaneously in all of the cells. The sixteen cells shown in Fig. 9 and in optical section in Fig. 10 are all of approximately the same size. Except for the occasional presence of the polar bodies at this stage it would be impossible to distinguish the animal from the vegetal pole. The cleavage cavity is now larger and it no longer opens widely to the exterior.

In subsequent cleavage stages division does not take place simultaneously in all of the cells; this is shown, for example, by Fig. 11, in which twenty cells are present, some of which are considerably larger than the others. In the eggs represented in Fig. 12 about forty-eight cells are present and some of these are larger than others, indicating that with them division has been delayed. The egg shown in Fig. 12 has been flattened by the cover glass, so that its apparent diameter is greater than normal; at the same time the blastomeres are separated from one another in an abnormal manner. At all stages the blastomeres are but loosely joined together and they break apart at the slightest pressure. In the later development I have found many embryos which are about one-half or one-quarter the size of the normal embryo, and it seems likely that such embryos have developed from isolated blastomeres of the two- or four-cell stage.

After this brief description of the cleavage, I think it will be quite apparent to everyone that it would be extremely difficult, if

not quite impossible, to work out the cell lineage of *Terebratulina*, even with an abundance of most favorably preserved material. With the material at my disposal such work was wholly out of the question. In the blastula, even at the time when gastrulation begins, one is struck by the great uniformity in size and quality of all the cells. I have found it quite impossible to distinguish any difference between the cells which invaginate and those which do not until after the gastrulation is well advanced.

### III. GASTRULATION AND FORMATION OF BODY LAYERS AND CAVITIES.

Gastrulation occurs by typical invagination, and at the time when the infolding begins there is no difference in the cells at the two poles (Figs. 13 and 37). The infolding continues until the inner layer comes into contact with the outer one and the blastocoel is entirely occluded (Fig. 14 *et seq.*). During this process there is a decided change in the character of the cells of the inner layer; they become very much shorter and henceforth are cuboid or rounded in shape; the cells of the outer layer remain columnar in shape and are very long, so that the ectoderm is quite thick. Large deeply staining granules are found at the free ends of all the cells, both those which are invaginated and those which are not, and in the invaginated cells these granules are so dense that they frequently obscure the nuclei and cell boundaries. In the ectoderm these granules lie on the outer side of the nuclei (Fig. 37 *et seq. Pg.*), while the inner ends of the cells are left free from granules and nuclei and hence are very clear. I suggest that these granules may be associated with the cilia, which in life cover the embryo and line the enteron and coelom (see Morse, '73).

Almost as soon as the inner layer comes into contact with the outer one—*i. e.*, when the infolding is complete—the innermost portion of the archenteron becomes slightly constricted from that portion lying nearer the blastopore. This constriction is deepest anteriorly, least marked posteriorly, while it is about equal on the left and right sides of the archenteron (Figs. 14, 15, 16, 38). On the anterior side this constriction develops into a partition wall, which grows downward and backward into the archenteron, shutting off the enteron above from the enterocoel below (Figs. 16, 20, 42*a* and 42*b*). So far as I am able to determine this partition wall

is always but one cell thick (Figs. 40-42), though in the earlier stages of its development it represents a fold in the wall of the archenteron (Figs. 42*a*-42*b*). The backward growth of this partition wall continues until the enteron is entirely separated from the enterocoel save for a narrow slit-like communication at the posterior end (Figs. 20, 24).

While the enteron is thus being separated from the enterocoel the blastopore is gradually closing and the whole embryo is becoming flattened in a dorso-ventral direction and elongated antero-posteriorly. The blastopore is at first a circular opening; it then becomes narrowed from side to side and apparently elongated antero-posteriorly (Figs. 17-21). The blastopore groove thus formed is shallow posteriorly and deepest at its anterior end where it opens into the enterocoel and enteron (Fig. 17). This groove continues to grow narrower and to be filled up at its posterior end until it becomes a mere slit, opening by a small pore near its anterior end into the enterocoel (Figs. 21, 22). Finally this pore also closes (Fig. 24) and the enterocoel and enteron are completely shut off from the exterior, though still communicating with each other by a narrow opening in the region posterior to where the blastopore closed (Figs. 24 and 46, 47). The blastopore groove persists for some time after the pore has closed but ultimately disappears, though a depression is left at the anterior end of this groove which becomes a part of the anterior mantle furrow; it is probable that at this very point the oesophageal invagination occurs at a stage after the fixation of the larva (see p. 56).

In stages in which the blastopore is still circular the enterocoel is but little larger than the enteron (Figs. 14 and 38). In looking at an entire egg of this stage from the oral side one sees two cavities of about the same diameter, one above the other, which communicate with each other by a wide opening; the cavity nearest the blastopore is the enterocoel, the one nearest the aboral side the enteron. In an older stage (Fig. 17) in which the blastopore has begun to narrow one still sees that these two cavities are of nearly the same diameter. As the enteron becomes separated from the enterocoel, however, the latter becomes much more extensive than the former, and an oral view of an embryo at this stage shows the enterocoel lying on the oral side of the enteron and entirely surrounding it except on the aboral side (Fig. 21, also optical sections, Figs. 19 and 20). This rapid enlargement of the enterocoel

is due in large part to the change in shape of the embryo, which becomes flattened in a dorso-ventral direction and enlarged in its other axes. Associated with the growth of the enterocoel is an important change in the character of its bounding cells; at first they form a quite regular, cuboid or columnar epithelium (Figs. 14-16 and 40-42a), but as the enterocoel increases in size the epithelium becomes less regular, particularly at the anterior end, and here many mesenchyme cells come to lie in the cavity of the enterocoel (Figs. 20, 21, 42b, 43). Later such mesenchyme cells are found generally throughout most of the coelom. The cells bounding the enteron remain cuboid or columnar throughout the development.

With the flattening of the embryo and the closure of the blastopore, the ventral wall of the enteron is brought into contact with the ectoderm at the place where the blastopore closes (Figs. 24 and 44-47), and consequently the enterocoel is here divided into right and left cavities, which however still communicate with each other at the anterior end and open into the enteron posteriorly (consult Figs. 43-47 which are transverse sections of an embryo of the stage shown in Fig. 24, Fig. 43 being the most anterior section drawn and Fig. 47 the most posterior). Very soon after this stage the communication between the enteron and the enterocoel is completely cut off and the definitive coelom is thus formed, consisting of two sacs, still opening into each other anteriorly and posteriorly but separated throughout the middle region of the embryo (consult Figs. 48-52 which are cross sections, in order from the anterior to the posterior region, of an embryo of about the stage shown in Fig. 28).

The gastrulation and formation of body cavities in brachiopods has been observed heretofore only by Kowalevsky. A comparison of the method of gastrulation and coelom formation in *Terebratulina* with Kowalevsky's observations on *Cistella* and other brachiopods reveals many resemblances and some interesting differences. Kowalevsky found that the gastrula was formed by invagination in *Cistella*, *Terebratula* and probably *Terebratulina*; by delamination or ingression in *Thecidium*. In all cases, however, he describes the coelom as arising as two lateral pouches from the archenteron in the same manner as in *Sagitta*, viz., by the folding into the archenteron of two lateral partitions. In this way the archenteron is divided into three portions, a median one which becomes the

enteron and two lateral ones which form the coelom. It is difficult to determine from Kowalevsky's figures from which portion of the archenteron these lateral partitions arise, but there can be no doubt that they are regarded as *folds* of the archenteric wall (see his Fig. 6), nor that they divide the archenteron into three cavities, the enteron and two coelom sacs. In both of these respects *Cistella* is very unlike *Terebratulina*; in the latter the archenteron is first divided into two cavities and not three (the enterocoel is for a long time unpaired), and the single partition wall by which this division is brought about consists of a single layer of cells and not a plication of the archenteric wall (though in its earliest stages this partition wall probably represents such a plication, Fig. 42a). The former of these differences is perhaps not so great as would at first thought appear, being principally due to the fact that in *Terebratulina* the enteron occupies but a small part of the archenteron, and hence the partition wall which separates it from the enterocoel leaves the latter a large unpaired cavity, whereas in *Cistella* the division of the archenteron is more nearly equal and when completed separates two lateral enterocoel pouches from the median enteron. But one cannot overlook the fact that according to Kowalevsky two partition walls are formed in *Cistella*, whereas but a single one is found in *Terebratulina*. Moreover these partitions are lateral in position according to Kowalevsky, whereas in *Terebratulina* the single partition grows out from the anterior wall and merely curves around on to the lateral walls of the archenteron (Fig. 16). The difference in the structure of this partition in *Cistella* and *Terebratulina* is also important; in the former it consists of a double layer of cells, in the latter of a single layer; in *Cistella* the wall of the enterocoel sacs lying next to the enteron becomes the splanchnic layer of the mesoblast, in *Terebratulina* the splanchnic mesoblast is derived from mesenchyme cells. Before attempting to explain these important differences between *Cistella* and *Terebratulina* in the formation of the coelom it would be well to know that they actually exist, and it seems highly desirable that the embryology of *Cistella* should be reinvestigated with the aid of modern histological methods.

The differences between *Terebratulina* and *Sagitta* in the mode of forming the coelom are of interest since they remove one important argument for the supposed relationship between Brachipoda and Chætognatha.

#### IV. ORIENTATION OF THE EMBRYO AND ESTABLISHMENT OF DEFINITIVE AXES.

It is well known that previous investigators of the embryology of the brachiopods have found the proper orientation of the embryo one of their most perplexing problems. The complete closure of the blastopore at a relatively early stage and before many landmarks have appeared by which its position relative to definitive organs could be determined, as well as the fact that both the oral and aboral sides of the embryo are very similar, has been chiefly responsible for this uncertainty of orientation. However if one studies carefully whole embryos of the critical stage when the last remnant of the blastopore is disappearing, the proper orientation of the embryo of a brachiopod is no more difficult than is that of any other animal.

In the stage shown in Figs. 23 and 24 the antero-posterior axis of the embryo is well defined, while the remnants of the blastopore are still present. The enlarged end of the embryo (to the right in Fig. 24) is anterior and gives rise to the head, while the posterior end (to the left in the figure) is narrowed and gives rise to the peduncle. The point where the blastopore closed (Fig. 24, *Br*) lies near the middle of the ventral side, while the blastopore groove runs backward almost to the posterior end of the embryo. Directly opposite the blastopore is a groove which runs transversely across the dorsal side of the embryo; this is the dorsal mantle groove, and the prominent ridge anterior to it is the dorsal mantle fold (Fig. 24, *Md*). If now Fig. 24 be compared with Figs. 20 and 16 it will be seen that the blastopore occupies the ventral-posterior region of the embryo, and that the anterior pole of the embryo is rounded while the posterior pole is pointed, the embryo being flattened on its postero-dorsal side. The prominent ridge opposite the blastopore in Figs. 16 and 20 corresponds with the dorsal mantle fold in Fig. 24. A comparison of these three figures further shows that the axis connecting the middle of the blastopore with the apex of the gastrula invagination (*e. g.*, *E* in Fig. 14) is ultimately bent on itself through an angle of more than 90°. It is difficult to say whether this bending of the gastrula axis is chiefly due to the forward shifting of the blastopore on the ventral side or to the forward shifting of the apex of the gastrula invagination, since there are no points in the embryo which may be

considered as fixed in position. It is highly probable however that both movements occur and that both the apical pole and the blastopore pole are shifted forwards, while the middle of the gastrula axis is shifted backwards, the gastrula axis thus being doubled on itself exactly as is the case, in Turbellaria, Annelida and Mollusca. Since the polar bodies have long since disappeared it is impossible to locate exactly on the embryo the point which corresponds to the animal pole of the egg. It is probable, however, that this point lies on the ectoderm directly opposite the apex of the gastrula invagination, and therefore anterior to the ridge which develops into the dorsal mantle fold. In the forward shifting of the apex of the gastrula invagination it is highly probable that this point is also shifted forward and continues to lie opposite the apex of the enteron. If this be true the animal pole of the egg coincides very nearly with the point where the line from *Ce* in Figs. 20 and 24 touches the ectoderm.

The bending of the gastrula axis which has just been described shows that *Terebratulina*, like most bilateral animals, belongs to the group designated by Hatschek ('88) Heteraxonia, and by Goette ('82) Hypogastric forms. Goette has divided bilateral animals into two groups: (1) the pleurogastric, in which the chief axis of the egg becomes the chief axis of the larva or adult, as in *Sagitta* and the echinoderms, and (2) the hypogastric, in which one of the "cross axes" of the egg becomes the chief axis of the larva or adult, as in worms, mollusks and arthropods. There can be no doubt that *Terebratulina* should be classed among the hypogastric forms, and if it be true, which however seems questionable, that *Sagitta* and the echinoderms belong to the pleurogastric type, it shows a very important difference between the embryo of the brachiopod and of the chætognath.

#### V. DEVELOPMENT AND ORGANIZATION OF THE LARVA.

There is of course no natural line of demarcation between the embryo and the larva, but for the sake of convenience we shall designate those stages which precede the closure of the blastopore as embryonic, while those which extend from the closure of the blastopore to the end of the free-swimming life we shall call larval stages.

The flattening of the embryo in the dorso-ventral axis and its

elongation antero-posteriorly have already been described. At the same time the embryo becomes wider at its anterior end and narrower posteriorly. The dorsal mantle groove and fold appear and the fold extends over on to the ventral side of the larva as a slight swelling on each side of the midline (Figs. 25 and 26). These are the halves of the ventral mantle fold and at first they are separated in the mid-ventral line by the blastopore groove (Fig. 26, *Bf*), while the blastopore remnant (*Br*) lies at the anterior end of this groove. Very soon after this stage the halves of the ventral mantle fold fuse with each other, thus obliterating the last trace of the blastopore groove, while a deep notch on the anterior side of the ventral mantle fold (Fig. 29, *O*) represents the place at which the blastopore remnant was last seen.

1. *The Mantle Fold* is at this stage a ring-like prominence which extends all the way around the larva (Figs. 29, 30, 31). This ring passes obliquely around the larva, being nearer the anterior end on the dorsal side and nearer the posterior on the ventral side (Fig. 31). Two mantle furrows are now plainly distinguishable, one in front of and the other behind the mantle fold. The anterior furrow is deepest on the ventral side, while the posterior one is deepest on the dorsal side (Figs. 29-31). With the appearance of the mantle, bounded anteriorly and posteriorly by these constrictions, the mantle furrows, three regions may be recognized in the larva, viz., the cephalic region, in front of the anterior mantle furrow, the mantle, between the anterior and posterior furrows, and the peduncular region, behind the posterior mantle furrow.

These constrictions, which I have called the anterior and posterior mantle furrows, continue to grow deeper but at no time do they form true septa which divide the coelom. The regions which they separate are not, therefore, segments, as Kowalevsky supposed. The larva is at this, and all other stages which I have studied, unsegmented, and the appearance of segmentation is due merely to the formation of the mantle from the middle region of the body.

The mantle becomes a very prominent ring around the body, and then its free edge is turned backwards until it surrounds the peduncular regions on all sides (Figs. 32-36). A space is left between the mantle and the peduncle which is the peduncular chamber (Figs. 34 and 36, *PC*). This chamber is a little deeper and wider on the dorsal than on the ventral side, which is due to the fact



that the posterior mantle furrow is deeper and is farther forward on the dorsal than on the ventral side (Fig. 31, *Fp*).

When the mantle has reached the limit of its backward growth it entirely covers the peduncle, the extremity of which nearly fills the circular opening of the mantle chamber (Figs. 34 and 36). This is the oldest stage which I have had opportunity to study. Morse ('71) has observed in detail the transformation of this larva into the adult. He figures a great many stages showing the manner in which the mantle is turned forward over the cephalic region, its free edge being directed forward and its originally internal surface becoming external. This happens after the larva has become fixed by the tip of its peduncle, and it is evident from Morse's figures and descriptions that the stage shown in my Figs. 34-36 is one of the last stages in the free-swimming life.

2. *The Cephalic Region* lies in front of the anterior mantle fold and is nearly hemispherical in shape, being however somewhat variable in form (consult Figs. 32-36), which is probably due to the fact that it is extremely contractile, as Morse has observed. At its anterior end and slightly toward the dorsal side is a shallow depression, the apical sense plate, which bears a tuft of long cilia in life (see Morse). The enlarged end of the enteron as well as a portion of the mesoderm and coelom extend into the cephalic region.

3. *The Peduncular Region* is cylindrical in shape and is contracted near its posterior end. This contraction is due to the fact that the coelom and mesoderm terminate abruptly some distance in front of the end of the peduncle (Figs. 34 and 36), and it is certainly not to be taken as constituting a fourth region of the larva, as Shipley ('82) suggests in the case of *Cistella*. The endoderm is continued as a solid cord of cells nearly to the end of the peduncle.

4. *The Ectoderm* covering the larva is unusually thick, though consisting of but a single layer of cells; these cells are however extremely long. Their inner ends are clear and free from nuclei and granules, so that on first examination a clear zone seems to separate the outer from the inner layer (Figs. 38 *et seq.*). Only on the anterior side of the mantle fold does the ectoderm become cuboid or squamous, while over the cephalic and peduncular regions it is particularly thick.

5. *Setæ Sacs*.—High columnar cells line the peduncular chamber,

and at four places (two median and two lateral) on the dorsal side of the mantle the epithelium is invaginated to form the setæ sacs (Figs. 34, 36, 56-64, *SS*). No traces of setæ are preserved in the material which I have examined, but there can be no doubt from Morse's ('73) account that these invaginations give rise to the lateral and median bundles of temporary setæ.

6. *Sense Plates and Ganglia*.—A little toward the dorsal side of the apex of the cephalic lobe is a depression in the ectoderm, and in this region the cells are deeply pigmented, especially at their free borders. This is the apical sense plate (*Scheitelplatte*) (Figs. 26, 28, 29, 31, 32, 34, 35, 36, 56, 57, 58, *CG*), and in life bears a tuft of long cilia (see Morse, '73), though no trace of these is left in the material which I have examined. At the base of the cells of this sense plate ganglion cells are cut off from the epithelial cells, but continue to lie in the ectoderm (Figs. 28, 36, 56, 57). These ganglion cells are small and I have been unable to observe their further development, but there seems no reason to doubt that they represent the cerebral ganglion.

A similar sense plate and ganglion is formed on the midventral line immediately posterior to the place where the blastopore remnant closed and in the region where the blastopore lips fused along the mid-line (Figs. 29, 31, 35, 58, 61, 62, *SG*). This is the ventral sense plate, and the cells of this plate are pigmented as are those of the apical plate; I think it probable that they bear a tuft of long cilia in life, although no one has observed this feature as yet. As in the case of the apical plate, ganglion cells are cut off from the basal ends of the epithelium of the ventral plate, and here again there seems every reason to believe that these ganglion cells become the suboesophageal ganglion. The oesophagus has not formed in the oldest larva which I have been able to study, but a slight invagination of the ectoderm immediately anterior to the ventral sense plate probably represents the earliest step in the formation of the oesophagus (Fig. 58, *O*). Heretofore no observations have been made on the early development of the nervous system. Neither Morse nor Kowalevsky observed any stages in the formation of the nervous system. Shipley has observed in the head region of *Cistella* a small clump of cells without granules, which he suggests may be a nerve ganglion; his Fig. 35 shows however that it lies entirely within the mesoderm, and it cannot therefore be a ganglion. Brooks has described in detail the nervous system of the larva of

Glottidia, but this system is already well formed in the earliest larva which he observed.

7. *Enteron*.—The cavity of the enteron is flask-shaped, the enlarged end lying in the cephalic region while the pointed extremity extends into the peduncle. In early larval stages the transverse diameter of the enteron is greater than its dorso-ventral diameter (Figs. 25 and 44-50); in later stages it becomes circular in cross section (Figs. 53-55), while in still later stages it becomes compressed laterally so that its greater diameter is in a dorso-ventral direction (Figs. 33, 35, 56-60). In the oldest stages which I have observed a diverticulum from the anterior end of the enteron grows out toward the ventral side, and at the same time an invagination of the ectoderm appears in the anterior mantle furrow, at the very point where the blastopore remnant disappeared, and grows in toward this diverticulum (Figs. 35 and 58). I presume that this is the first step in the formation of the oesophagus. During the whole of the larval period the enteron has no opening to the exterior. According to Morse ('73) the mouth is formed late in the metamorphosis, and while he does not describe the place or manner of its formation his Fig. 90 shows it at the anterior extremity of the young brachiopod. Kowalevsky ('74) also has described and figured what he considers to be the formation of the oesophagus at the anterior end of the cephalic lobe. From what I have observed I feel confident that the mouth is first formed on the ventral side, in the region of the anterior mantle furrow, and if it is later found at the anterior end of the young brachiopod, its change in position must have been brought about by secondary changes. Kowalevsky expresses some doubts as to whether the invagination observed by him at the anterior end of the cephalic lobe is really the oesophagus, and from its location I would suggest that it is the apical sense plate and cerebral ganglion rather than the oesophagus. My observation as to the location of the stomodæal invagination thus confirms Heider's ('93) theoretical suggestion and brings the brachiopod larva into close relationship with the trochophore.

The cells bounding the lumen of the enteron are cuboid in early stages and columnar in later ones (compare Figs. 43-50 with Figs. 56-60). These cells, enclosing a minute lumen, extend through the entire peduncular region (Figs. 36, 57, 58, 61-64).

From its earliest formation the enteron is in contact on its dorsal

side with the ectoderm, while laterally and on its ventral side it is bounded by mesoderm (Figs. 43-52, 58 and 61-63).

8. *Cœlom*.—For a long time after the division of the cœlom into right and left cavities by the flattening of the embryo and the closure of the blastopore these sacs communicate with each other both anteriorly and posteriorly (Figs. 43-47, 48-52, 53-55). In still later stages these communications are closed by the practical elimination of the cœlom in the cephalic and peduncular regions through the proliferation of mesenchyme cells (Figs. 56-63). The cœlom sacs, which are at first of nearly the same size both anteriorly and posteriorly (Fig. 25), become much constricted in the peduncular region while they still remain large in the head and mantle regions (Fig. 26). In the latter region they then become lobulated, often showing a trefoil condition (Figs. 27, 28), and with the further development of the dorsal and ventral mantle folds a lobe of the cœlom is sent into each of these folds (Figs. 29-33). At the same time the cœlom in the cephalic and peduncular regions grows smaller, while that in the mantle grows larger. Finally almost the entire cœlom is contained in the mantle, the portion in the head and peduncle being very small (Figs. 36 and 56-63). The posterior limits of the peduncular cœlom is marked by a narrowing of the peduncle, which probably represents the fourth "segment" of Shipley. The cœlom however is never segmented though it may be constricted in certain places. The constrictions shown in Figs. 27-31 are quite constant in position and are connected with the extension of the cœlom into the mantle lobes, but they never coincide in position with the superficial constrictions of the body (mantle furrows). In a few abnormal larvæ of the stage shown in Fig. 25 I have found each cœlom sac partially divided by mesenchyme cells into three cavities. That these divisions, however, have no real importance is shown by the fact that their number differs in different larvæ and is sometimes different on opposite sides of the same larva.

In the early larval stages the enteron is in close contact with the ectoderm on the dorsal side, while a collection of mesoderm cells on the ventral side of the enteron separates the two cœlom sacs and may be considered the rudiment of a ventral mesentery (Figs. 49, 50).

In later stages the cœlom is almost entirely obliterated, except in the mantle, and consequently the enteron is surrounded by

a dense mass of mesoderm cells, except on the dorsal side, where it is still in contact with the ectoderm (Figs. 56-64). At this stage therefore there can be no mesenteries since there is practically no coelom.

In early stages of larval life the mesoderm cells are mesenchymatous in the anterior region of the body and epithelial in the posterior regions (*cf.* Figs. 43-46). In the later stages the mesoderm cells of the posterior regions become more mesenchyme-like (Figs. 48-52 and 53-55), while in still later stages they become densely packed and pigmented and it is impossible to distinguish their cell boundaries (Figs. 56-64).

## VI. GENERAL CONSIDERATIONS AND CONCLUSIONS.

Although I am not one of those who expect to find phylogeny "writ large" in ontogeny, yet it may be worth while to point out the bearings of the development of *Terebratulina* on the supposed relationships of brachiopods. Since my own studies cover only the embryonic and larval periods, I shall of course limit to those periods the comparison of *Terebratulina* with other forms. Within these periods we may compare (1) the cleavage, (2) mesoderm and coelom formation, (3) orientation of embryo and larva, (4) the general morphology of the larva.

1. *The Cleavage.*—As has been said already, there is no evidence that the cleavage of *Terebratulina* resembles that of mollusks or annelids. It is now known that in a great many annelids and leeches and in all groups of mollusks except the cephalopods the cleavage is of a certain determinate or morphogenetic (Child, 1900) type. The principal characteristics of this type of cleavage are that the ectoderm is segregated in three quartettes of cells, that the greater part of the mesoderm appears in one cell (4d) of the fourth quartette, and that the remaining cells of the fourth quartette together with the basal cells (macromeres) constitute the endoderm, and finally that the elongation of the embryo takes place by the teleoblastic cleavage of certain cells in the ectoderm and mesoderm (first and second somatoblasts, 2d and 4d) and possibly also in the endoderm (endodermic derivations of 4d). In addition to these general characteristics of the cleavage of annelids and mollusks there are other characteristics less general in application, such as the derivation of the prototroch, the stomodæum, the cerebral

ganglia, etc., from certain cells of the ectoderm. Wilson ('99) has shown that many of the general characteristics mentioned above are applicable also to the cleavage of the Turbellaria.

With regard to some of these general characteristics it is impossible at present either to affirm or deny their presence in *Terebratulina*. For example, owing to the difficulty of identifying individual cells I cannot say whether or not the ectoderm is segregated in three quartettes. In fact I am wholly unable to recognize quartettes at all after the eight-cell stage. It is certain, however, that the mesoderm is not formed by teleoblastic growth from a single cell and that the embryo does not grow in length by the teleoblastic cleavage of two somablasts. Furthermore the cleavage of *Terebratulina* shows no resemblance to any type of determinate or morphogenetic cleavage which has yet been described, whether among annelids, mollusks, turbellarians, nematodes or ascidians. On the other hand it does resemble in some respects the indeterminate cleavage of echinoderms, Phoronis and ectoproctous Bryozoa.

2. *Mesoderm and Cœlom*.—The gastrulation occurs by typical invagination; however, this method of gastrulation is found in almost every great group of animals, and therefore no phylogenetic significance can be attributed to it. In the formation of the cœlom however the case is somewhat different. The method of mesoderm and cœlom formation in *Terebratulina* is totally unlike that which is found in annelids, mollusks, platyhelminths, nematodes and arthropods, while it shows certain resemblances to chætognaths and echinoderms. A more detailed comparison shows however that even these resemblances are not very close.

In echinoderms the enterocoel is formed at the inner end of the archenteron, while the enteron arises from that portion of the archenteron nearest the blastopore; in brachiopods the enteron is formed from the inner end of the archenteron, while the enterocoel arises from that part of the archenteron which in echinoderms gives rise to the enteron. It is evident therefore that no real resemblance exists between echinoderms and brachiopods in this respect.

In chætognaths the method of cœlom formation is more like that in brachiopods—in fact Kowalevsky supposed that the two were identical—and yet there are important differences here also. In *Sagitta*, according to both Kowalevsky ('71) and Hertwig ('80), two bilateral folds of the archenteric wall grow into the archen-

teron from its apex, thus dividing the cavity into a median one, the enteron and two lateral ones, the enterocoels. The stomodæum is said to open into the apical end of the enteron, directly opposite the blastopore, which has however closed at an earlier period. In *Terebratulina*, on the other hand, the enteron is separated from the single enterocoel by one partition which grows out from the anterior wall of the archenteron and divides the latter into a dorsal cavity, the enteron, and a ventral one, the enterocoel; only later, by the closure of the blastopore and the flattening of the embryo, does the enterocoel become divided through its middle region into right and left cavities, which, however, continue for some time to communicate with each other both anteriorly and posteriorly. Moreover the stomodæum in *Terebratulina* is formed in the position of the former blastopore and not on the opposite side of the embryo. Therefore, although there are certain general resemblances between the two, I cannot regard the coelom formation in chætogonaths and brachiopods as being more than analogous processes, and as such devoid of phylogenetic significance.

In *Phoronis*, according to Caldwell ('85), two pairs of coelomic cavities are formed by a modified type of enterocoel formation, which however bears no resemblance to that in *Terebratulina*. The anterior one of these cavities gives rise to the cavities of the epistome and lophophore, the posterior one to the chief body cavity.

Masterman's (1900) work on the development of *Phoronis* furnishes the most complete account of the early development of this interesting form which has yet been given.<sup>1</sup> In an earlier work ('97) he found that there were three separate and distinct coelomic cavities in the larva, a preoral or epistomal cavity, a collar or lophophoral cavity and a trunk cavity. In his later paper he describes the origin of these cavities; the first of these arises as a median outgrowth from the anterior side of the archenteron, the other two arise as paired masses of solid mesoderm cells in which cavities appear later. In the matter of the formation of the anterior or procœlomic cavity there is much resemblance between *Phoronis* and *Terebratulina*, but in the latter animal the mesocœlomic and metacœlomic cavities are entirely absent.

<sup>1</sup> Since the appearance of Ideka's (1901) work this statement is no longer true. Ideka has given by all odds the most complete account of the embryology of *Phoronis* yet published. (See postscript, p. 70.)

Very little is certainly known of the formation of the mesoderm and coelom among the Bryozoa. In the Ectoprocta the larval form is usually solid, the coelom and enteron having undergone extensive if not complete degeneration, while in those forms in which the coelom is still preserved its method of origin is highly peculiar. For example, in the Phylactolæmata the central cavity of the embryo is generally considered to be the coelom, although at the stage at which it appears there is neither endoderm nor enteric cavity in the embryo (see Korschelt and Heider's Text-Book).

Among the Endoprocta the mesoderm arises in *Pedicellina*, according to Hatschek, from two pole cells which appear at the posterior edge of the blastopore; these cells by repeated divisions give rise to two short mesoderm bands, and from these bands mesoderm cells arise which fill the space between the ectoderm and the endoderm. It appears therefore that no direct comparison can be made between *Terebratulina* and the Bryozoa in the matter of the formation of mesoderm and coelom.

3. *Orientation of Embryo and Larva.*—As has been pointed out already the relation of the chief axis of the gastrula to the chief axis of the larva is the same as is found in all Heteraxonia (Hatschek) or Hypogastric forms (Goette). The animal pole of the egg and the apical pole of the gastrula become the cephalic pole (*Hirnsfeld*) of the larva, while the blastopore comes to lie on the ventral side. Such a relation of the embryonic and larval or adult axes is of very general occurrence, being found at least in all Trochozoa (Hatschek). Moreover in having a blastopore which becomes narrow from side to side and then eloses from behind forward, and also in the formation of the stomodæum at the place where the blastopore closed, *Terebratulina* agrees with a large number of bilateral animals belonging to widely different phyla. These characters are so general, therefore, as to be of little value in determining the affinities of the brachiopods. Regarding the apical sense plate as anterior and the suboesophageal sense plate as ventral in position, it follows that the peduncle is posterior and the mantle folds dorsal and ventral; consequently even after the metamorphosis the peduncle is posterior, and the valves which are formed by the mantle folds are dorsal and ventral, while the opening of the valves is anterior. This orientation is the commonly accepted one and is directly opposed to Caldwell's ('82) remarkable views, according to which both valves and the peduncle are ventral in position.



4. *General Morphology of Larva.*—The resemblances between the early embryos of *Terebratulina* and those of other metazoa are so general in character that they afford little assistance in determining the affinities of the brachiopods. We must therefore rely largely upon the structure of the larva and of the adult for the solution of this problem.

(a) *Comparison with Trochophore.*

Among the chief characteristics of the trochophore larva, as enumerated by Hatschek ('88, p. 307), are the following :

- I. (1) Bilateral symmetry, (2) mouth on ventral side, (3) anus near posterior end, (4) shape ovoid.
- II. (5) Apical tuft of cilia, (6) preoral ciliated band (Trochus), (7) postoral ciliated band (Cingulum), (8) adoral ciliated zone, (9) ventral ciliated furrow between mouth and anus, (10) small cilia over general surface of larva.
- III. (11) Epithelial nervous system, (12) apical plate (*Scheitelplatte*), ganglion and sense organs, (13) œsophageal nerves and buccal (ventral) ganglion, (14) ventral (and sometimes dorsal) longitudinal nerves.
- IV. (15) Alimentary canal (œsophagus, stomach and intestine) horseshoe-shaped and ciliated throughout, (16) stomach retort-shaped, (17) intestine reaches to posterior end of body.
- V. (18) Mesoderm partly mesenchymatous, partly epithelial, (19) mesenchyme gives rise to branched connective tissue cells and thread-like or branched muscle cells, (20) ventral and dorsal longitudinal muscle pairs, (21) preoral and postoral ring muscles, (22) dilators and constrictors of œsophagus and intestine, (23) mesothelium gives rise to the paired protonephridium, which is a longitudinal ciliated tube closed at the anterior end by terminal cells, and opening posteriorly on the ventral side in front of the anus, (24) paired coelomic sacs at the posterior end.

Of these characteristics, numbers 5, 6, 7, 8, 11, 12, 13, 15, 16, 17 and 23 are undoubtedly the most important, and all of these except the last are found also in brachiopod larvæ. All investigators of the embryology of brachiopods have described the apical tuft of cilia (5); the preoral ciliated band (6) is probably

represented in the brachiopod larva by the circle of longer cilia found at the base of the preoral lobe (see Kowalevsky's figures of *Argiope* larvæ); the postoral ciliated band (7) is probably represented by the mantle, which attains a much greater development in the brachiopod larva than in the ordinary trochophore; the adoral ciliated furrow (8) is represented by the anterior mantle furrow; the fact that adult brachiopods have an epithelial nervous system (11) has long been known, and I have observed the beginnings of such a nervous system in the larva of *Terebratulina*; I have also observed (p. 55) the apical plate and ganglion (12) and the ventral plate and ganglion (13) in *Terebratulina*; only the beginnings of the cesophageal invagination are shown in the oldest larva which I have studied, but it is evident from its position that after it joins the stomach the alimentary canal will be horseshoe-shaped (15); the stomach in *Terebratulina* larvæ is retort-shaped (16) and the intestine reaches to the posterior end of the larva (17).

In addition to these more important characteristics the larvæ of *Cistella*, *Thecidium* or *Terebratulina* agree with the trochophore in the possession of the following characteristics: Bilateral symmetry (1), blastopore and *anlage* of mouth on ventral side (2), ventral blastopore groove (9) and general ciliation of body (10), mesoderm partly mesenchymatous, partly epithelial (18); finally ventral and dorsal longitudinal muscles (20) are present in the peduncle of *Cistella*. These brachiopod larvæ also agree with many chætopod larvæ in the possession of ectodermal seta sacs and provisional setæ.

The points in which the larvæ of testicardinate brachiopods differ most from the trochophore are in the absence of mouth and anus and the lack of a protonephridium. In the Ecardines however both mouth and anus are present during larval life, and in all brachiopods a single pair of nephridia appears after the larval period. The absence of these larval structures therefore indicates a retardation or less perfect development of the larval brachiopod as compared with the typical trochophore. I believe therefore that the brachiopod larva belongs unquestionably to the trochophore type.

(b) *Comparison with Actinotrocha.*

The larva of *Phoronis*, while showing many peculiarities, bears a most decided resemblance to the trochophore. Among its principal characteristics may be enumerated the following:

- I. (1) There are three sections of the body: (a) the preoral lobe, (b) the postoral section (collar) which carries tentacles, and (c) the posterior or anal section (trunk); (2) the preoral lobe probably represents the umbrella of the trochophore; (3) the cilia at its margin probably correspond to the preoral ciliated band (Trochus), while (4) the postoral ciliated zone (collar) which carries the tentacles probably corresponds to the postoral band (Cingulum) of the trochophore; (5) this postoral ciliated zone (Cingulum) runs obliquely around the body, being further posterior on the ventral than on the dorsal side; (6) tentacles appear near the ventral midline and fresh pairs are added dorsally.
- II. (7) There is an epithelial nervous system, (8) an apical plate, ganglion and (in some species) eye spots, and (9) an oesophageal commissure.
- III. (10) The coelom is composed of an anterior unpaired cavity and two pairs of cavities posterior to this (Masterman);<sup>1</sup> (11) the anterior coelom sac arises as an enterocoel, the posterior paired ones as schizocoels; (12) there is one pair of protonephridia, which end blindly internally in connection with excretory cells.
- IV. (13) There is a ventral invagination posterior to the zone of tentacles and a peculiar metamorphosis by the evagination of this invagination; (14) during metamorphosis the tentacles turn forward, and (15) the anus comes to lie on the dorsal side of the mouth, the intestine thus forming a loop.

Comparing now the larvæ of brachiopods with the Actinotrocha we find that, in addition to the general resemblances to the trochophore which both show, there are the following special resemblances between the two: (1) In both brachiopods and Actinotrocha the postoral ciliated zone (Cingulum) is greatly enlarged and runs obliquely around the body, being farther posterior on the ventral than on the dorsal side. (2) In both cases this forms the mantle or lophophore, though the tentacles or cirri which are borne upon it appear much earlier in Actinotrocha than in the brachiopod larva. (3) Brooks has shown that in *Lingula* the ventral pair of

tentacles appears first and that successive pairs of tentacles are added dorsally, exactly as in *Actinotrocha*. (4) In the metamorphosis the mantle (lophophore) is turned forward over the preoral lobe in exactly the same way in both cases. These are extremely important resemblances, and in themselves lend support to the view that *Phoronis* and the Brachiopoda are closely related.<sup>1</sup>

On the other hand, according to Masterman's ('97 and 1900) recent work on *Actinotrocha*, there are certain important respects in which *Actinotrocha* differs decidedly from the brachiopod larva: (1) The coelom consists of an anterior unpaired cavity and of two pairs of cavities, one of which lies in the lophophore and the other in the trunk region. The anterior unpaired cavity somewhat resembles in position and method of origin the anterior portion of the enterocoel of *Terebratulina*, but the lophophoral and trunk cavities of *Actinotrocha* differ from the mantle and peduncular coelom of *Terebratulina* in that the latter are a part of the enterocoel and are never completely separated from one another, whereas in *Actinotrocha* they arise as schizocoels and are always separate. (2) *Actinotrocha* also has rudiments, at least of a second pair of nephridia. (3) It also has two endodermal outgrowths from the anterior portion of the enteron, which are composed of large vacuolated cells, and are homologized by Masterman with the notochord of the Hemichorda.<sup>2</sup>

I have had no opportunity of studying the later stages in the development of the brachiopod, in which alone the two last-mentioned structures might be looked for, and cannot therefore determine whether there are real differences between the brachiopod and *Phoronis* in these respects. With regard to the differences shown by the coelom, one must bear in mind the fact that in the brachiopod larva the coelom almost entirely disappears, except in the mantle, and a segmentation of the coelom in later stages could not therefore be observed, even if it had at one time existed in the ancestors of the brachiopods. There can be no doubt however that in *Terebratulina* the entire coelom arises from a single enterocoel, in which respect there is a decided difference between the brachiopod and *Phoronis*. The resemblances mentioned above

<sup>1</sup> The presence of "plasmic corpuscles" (Ideka, 1901) in the blastocoel of both forms is another interesting resemblance (see p. 45).

<sup>2</sup> See postscript, p. 70.

however are so important and extend to such details that I am inclined to accept the view that *Phoronis* and the Brachiopoda are related, and to look to future work on the development of both of these groups to harmonize the apparent differences between them.

(c) *Comparison with Larval Polyzoa.*

Brooks in particular has emphasized the resemblance between the larvæ of Polyzoa and Brachiopoda, basing this comparison, however, rather upon the external characters in which both resemble the trochophore than upon a detailed comparison of internal structure.

*Ectoprocta.*—It is extremely difficult to compare larval brachiopods with larval ectoprocts, owing to the great variety of forms presented by the latter, their many secondary characters, and the conflicting accounts of their structures and homologies which have been given by various authors. There is some reason for believing however that the ectoproct larva belongs to the trochophore type, and that the following parts of the two may be homologous: (1) The retractile disk may correspond (at least in part) to the apical plate, (2) the corona in part to the trochus, (3) the sucker to the trunk of the trochophore, or to the ventral evagination of Actinotrocha. Furthermore one may trace a certain resemblance between the invaginated sucker of *Bugula* and *Lepralia* and the peduncle and mantle of *Terebratulina*. In both cases attachment takes place by the peduncle, while the covering folds (mantle in the case of brachiopods) are turned forward as the peduncle is protruded. However the degeneration and modification of structures, both in the larval stages and in the metamorphosis, are so extreme that any attempt at the present time to trace homologies between larval Ectoprocta and other forms must be accompanied by a lively imagination and a ready facility in guessing.

There is good evidence in the degeneration of the intestine and coelom of the ectoproct larva, and in the general degeneration which accompanies its metamorphosis, that we are dealing with a highly modified type of development, which is little likely to throw light upon the affinities of the Polyzoa. However the resemblances between the adult Polyzoa and *Phoronis* and the Brachiopoda is such as to warrant the conclusion that these groups are at least remotely related to one another.

*Entoprocta.*—Among larval entoprocts there are few, if any, undoubted homologies with either the trochophore, the actinotroch,

or the brachiopod larva. It is possible that the ciliated disk of *Pedicellina* and *Loxosoma* is homologous with the retractile disk of the ectoproct larva and with the apical plate of the trochophore, and that the margin of the vestibule (ciliated ring) in the former corresponds to the trochus of the latter, but these possible homologies are too hypothetical to be affirmed with any degree of assurance.

5. *Conclusions.*—Neglecting the older views as to the affinities of the brachiopods with lamellibranchiate Mollusca, which were founded merely upon superficial resemblances, we find that within recent times the brachiopods have been associated, at different times and by different authors, with Chætopoda, Polyzoa, Chætogonatha and Phoronis.

Both Morse ('73<sup>a</sup>) and Kowalevsky ('74) independently reached the conclusion that the brachiopods are chætopod annelids. Morse says in summing up his work on the subject ('73<sup>a</sup>, p. 57): "We must regard the brachiopods as *ancient cephalised chætopods*, while *Serpula*, *Amphitrite*, *Sabella*, *Protula* and others may be regarded as *modern* (later) *cephalised chætopods*"; and Kowalevsky ('74) maintained that the brachiopods ought to be considered simply as an order of the annelids, which present at least as many resemblances to the chætopods as do the leeches.

Morse has enumerated twenty-four characteristics in which brachiopods resemble more or less closely Vermes, sedentary annelids and Gephyreans. Kowalevsky also names a considerable number of points in which brachiopods resemble chætopods. Some of these features are not actually characteristic of the brachiopods, as, for example, the segmentation of the larva; others are of such a general character as to apply to almost all Bilateralia, as Brooks has shown, while still others represent real resemblances between the brachiopod larva and the trochophore. The trochophore larva however is of such wide occurrence among bilateral animals, that the mere classification of the brachiopods among the Trochozoa throws no light upon the nearer affinities of this group.

Huxley, Lankester, Claus and others have regarded the brachiopods as more or less closely related to the Polyzoa, and Brooks in particular has held that the two groups belong to the same phylum and class. "The organization of the *Lingula* larva," he says, "shows that it is not merely like a Polyzoon, but that it actually is one; as much so as the hydra stage of an Hydro-Medusa is a

Hydra, or the tailed larva of Botryllus is an Appendicularia, and more so than a tadpole is an urodellian Batrachian." This close relationship he bases largely upon the external resemblances between the larvæ of *Thecidium* and various Polyzoan larvæ. It seems to me that some of these resemblances are real homologies, but on the other hand the differences between these larvæ, as well as between the adults of these two groups, are so great that it would be inadvisable to place them together in the same class; though I believe they should be placed in the same phylum. Moreover it seems to me that Brooks' view, that the Polyzoa are the ancestral form of which the Brachiopoda are a specialization, is just the reverse of the real relationship; larval as well as adult Brachiopoda show less specialization and certainly less degeneration than the Polyzoa.

The resemblances of the brachiopod larva to the Molluscan veliger, upon which Brooks lays emphasis, are in the main the same as the resemblances to the trochophore, the veliger and trochophore belonging to the same type of larva.

The idea that the brachiopods are related to the chætognaths, which was suggested by Bütschli and Hertwig ('80) and maintained by van Bemmelen ('83), has little more in its favor than the supposed resemblance in the method of formation of the coelom and in certain histological details.

So far as the formation of the coelom is concerned, I have already pointed out the fact that in *Terebratulina* it forms in a very different manner from what obtains in *Sagitta*, and as for the histological resemblances they are by no means confined to the two groups in question. On the other hand there are so many important differences between the two groups, both in their embryology and in their adult structure, that one could as well maintain the affinity of the Brachiopoda with Echinodermata, Enteropneusta or Chordata, as with Chætognatha.

Caldwell ('82) first pointed out in detail the resemblances between *Phoronis* and the Brachiopoda. In this paper he has urged "an entirely new view of the homologies of the body surfaces in Brachiopoda." He regards the Brachiopoda as fixed by their ventral surface, and both valves of the shell as ventral in position, the peduncle of the brachiopod corresponding to the ventral invagination of Actinotrocha. While there are some facts which may be urged in favor of this view there are many which may be used

against it. The fact that in both *Phoronis* and *Lingula* the intestine forms a loop, the anus opening near the mouth, and that fixation takes place by the posterior extremity, has led to Caldwell's view as to the homologies of the body surfaces in the brachiopods. On the other hand the ventral mantle fold of *Terebratulina* forms directly across the region where the blastopore lips fused and immediately posterior to the place where the blastopore remnant closed and where the mouth later appears. Upon the anterior face of this fold the suboesophageal sense plate and ganglion appear; there can be no doubt therefore that this fold is ventral in position. The dorsal mantle fold appears at a very early stage (Figs. 16 and 20) on the apical side of the gastrula and just posterior to the chief gastrula axis; it is impossible therefore that it should be considered as ventral in position. *Furthermore the mantle folds of the brachiopod correspond to the zone which bears the tentacles in Actinotrocha* (collar, Masterman) *and not to the margins of the ventral invagination*; and since the mantle folds surround the body posterior to the mouth, both of them cannot be ventral in position. Whether the peduncle is ventral or not cannot perhaps be determined with certainty until we know the embryology of a brachiopod in which the anus and terminal portion of the intestine are present. In *Lingula*, as is well known, the anus opens near the mouth and on the left side; in *Crania* it is terminal in position, and the embryology of either of these forms should throw light on this question as to the morphological position and homologies of the peduncle. Brooks' work on *Lingula* deals only with stages in which the anus and the intestinal loop are already present, and one cannot therefore tell at what point relative to the blastopore the anus appears and how the loop is formed. It is certain however that the ventral invagination and remarkable metamorphosis of *Actinotrocha* are coenogenetic rather than phylogenetic characteristics, and that parallel phenomena need not be expected in other groups of animals. Furthermore it is certain that the peduncle in *Terebratulina* is derived from that portion of the gastrula which is posterior to the blastopore; I do not see therefore how it can be regarded as ventral in position. But however this problem of the relation of the peduncle of the brachiopod and the ventral invagination of *Actinotrocha* may be decided by future work, it seems to me that the affinities of *Phoronis* and Brachiopoda are well established. I agree therefore in the main with the views of Caldwell, Lang and Blochman, and



more particularly with the position of Heider, as to the affinities of the brachiopods. The relationship between Phoronis, Bryozoa and Brachiopoda seems to me sufficiently close to justify the placing of them in the same phylum, though not in the same class, as Lang has done.

#### POSTSCRIPT.

Since this paper was written I have seen Ideka's (1901) very important contribution on the "Development, Structure and Metamorphosis of Actinotrocha." Ideka's work is in all respects the most thorough and extensive which has yet been done on the development of Actinotrocha, and in many very important points he differs decidedly from Masterman. Some of the differences between Actinotrocha and the brachiopod larva, which are pointed out on p. 65, disappear in the light of this work. For example, Ideka finds that there is but one complete septum in the body, that between the collar and the trunk, while the cavities of the preoral lobe and collar are in communication through a very incomplete septum. Furthermore Ideka finds no trace of a second pair of nephridia or of a "proboscis pore," such as Masterman described, while the two "chorda" diverticula of Masterman (Diplochora) are represented by a single unpaired diverticulum in the Japanese species. Whether this is a glandular or skeletal structure is left an open question.

With the exception then of the single septum between the collar and the trunk regions there are no important differences between Actinotrocha and the brachiopod larva. This septum occupies a position in Actinotrocha corresponding to the posterior mantle furrow of the brachiopod larva, and it would be interesting to know whether, in stages of the brachiopod larva later than those which I have studied, any trace of a septum can be found in this position.

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## REFERENCE LETTERS.

- Bc*, Blastocœl.
- Bf*, Blastopore groove.
- Bp*, Blastopore.
- Br*, Blastopore remnant.
- C*, Cœlom.
- Ce*, Enterocœl.
- Cc*, Cephalic Cœlom.
- Cm*, Mantle Cœlom.
- Cp*, Peduncular Cœlom.
- Ccm*, Cephalic and Mantle Cœlom.
- Cmd*, Dorsal extension of Mantle Cœlom.
- Cmv*, Ventral extension of Mantle Cœlom.
- CG*, Apical Sense Plate and Cerebral Ganglion.
- D*, Dorsal.
- DA*, Dorsal-Anterior.
- E*, Enteron.
- Em*, Egg Membrane (ectoplasmic layer).
- Fa*, Anterior Mantle Furrow.
- Fp*, Posterior Mantle Furrow.
- Gc*, Gastrocœl.
- M*, Mantle.
- Md*, Dorsal Mantle Fold.
- Mv*, Ventral Mantle Fold.
- mc*, Mesenchyme.
- O*, Point where blastopore closed and œsophageal invagination appears.
- P*, Peduncle.
- Pb*, Polar Bodies.
- PC*, Peduncular Chamber.
- Pg*, Dark Staining Granules.
- SG*, Ventral Sense Plate and Sub-œsophageal Ganglion.
- SS*, Setæ Sacs.
- V*, Ventral.
- VP*, Ventral-Posterior.

## DESCRIPTION OF FIGURES.

All the figures illustrating this paper were drawn with Camera Lucida at the stage level under a Zeiss Apochromat. Homog. Immers. Obj. 3mm. Comps. Occ.

4. In the process of reproduction they have been reduced about one-third.

## PLATE I.

Fig. 1. One-cell stage; polar body in process of being formed; egg elliptical; ectoplasmic layer surrounds egg and polar body.

Fig. 2. Two-cell stage; one cell larger than the other; three polar bodies present.

Fig. 3. Transitional stage between two-cell and four-cell stages; showing overlapping of certain cells and "spiral" character of cleavage.

Fig. 4. Four-cell stage, two cells (at right) larger than the other two; protoplasmic areas surrounding nuclei shown; two polar bodies lie in the polar furrow.

Fig. 5. Eight-cell stage, apical view; three polar bodies at animal pole.

Fig. 6. Eight-cell stage, side view; one polar body at animal pole.

## PLATE II.

Fig. 7. Eight-cell stage, apical view; each cell indented at periphery; polar furrows at right angles to each other at opposite poles.

Fig. 8. Seven-cell stage; irregular cleavage; animal pole indicated by three polar bodies.

Fig. 9. Sixteen-cell stage, apical view; two polar bodies at animal pole.

Fig. 10. Sixteen-cell stage, optical section, showing blastocoel, ectoplasmic layer (*Em*) and polar body or yolk spherule between two of the cells.

Fig. 11. Twenty-cell stage; some of the cells elongated and probably dividing yolk spherules within blastocoel.

Fig. 12. About forty-eight-cell stage; egg flattened by pressure and the blastomeres partially separated.

## PLATE III.

Fig. 13. Early invagination stage, optical section.

Fig. 14. Gastrulation completed; blastocoel obliterated; gastrocoel partially divided into enteron (*E*) and enterocoel (*Ce*).

Fig. 15. Optical section of older embryo, viewed from posterior; enteron still further constricted from enterocoel.

Fig. 16. Optical section of embryo of same stage as preceding, lateral view, showing anterior extension of enterocoel and partition wall growing down on anterior side between enteron and enterocoel.

Fig. 17. Oral view of embryo, showing elongated blastopore opening at its anterior end into the enterocoel and enteron; the enterocoel but little larger than the enteron.

Fig. 18. Antero-ventral view of an embryo of about the same stage as the preceding.

#### PLATE IV.

Fig. 19. Optical section of older embryo, viewed from posterior; showing the enteron separated from the enterocoel.

Fig. 20. Optical section of an embryo of same stage as preceding, lateral view; showing the enteron almost entirely separated from the enterocoel.

Fig. 21. Oral view of an embryo of about the same stage as the preceding; the blastopore narrower than in preceding stages; the enteron completely cut off from the enterocoel except in the region of the blastopore; mesenchyme cells (*mc*) line the anterior part of the enterocoel.

Fig. 22. Oral view of an older embryo in which the blastopore has closed to a narrow groove except for a small opening near its anterior end; mesenchyme cells are abundant in the anterior and posterior parts of the enterocoel; mantle folds show at the sides of the embryo.

Fig. 23. Aboral view of an embryo of the same stage as the preceding, showing dorsal mantle fold (*M*).

Fig. 24. Optical longitudinal section of an embryo in which the blastopore has completely closed, leaving however on the ventral surface the blastopore remnant (*Br*) and groove; the dorsal mantle fold (*Md*) and furrow are shown on the dorsal side; the enteron still communicates with the enterocoel at its posterior end.

#### PLATE V.

Fig. 25. Dorsal view of a larva in which cephalic, mantle and peduncular regions are well defined.

Fig. 26. Ventral view of an older larva, showing the ventral mantle folds meeting in the region of the blastopore groove (*Bf*); the blastopore remnant (*Br*) lies in a notch on the anterior side of the mantle fold.

Fig. 27. Dorsal view of a slightly older larva, showing the increased prominence of the mantle and the lobulation of the coelom.

Fig. 28. Optical longitudinal section of a larva of the same stage as the preceding, showing the dorsal and ventral mantle folds (*Md* and *Mv*); apical sense plate and ganglion; enteron and coelom.

Fig. 29. Ventral view of an older larva, showing the ventral mantle folds fused in the midline; the anterior and posterior mantle furrows are shown as shaded lines; in the anterior mantle furrow the place at which the blastopore remnant disappeared and where the oesophageal invagination will occur is marked (*O*); the apical and ventral sense plates (*CG* and *SG*).

- Fig. 30. Dorsal view of a larva of the same stage as the preceding, showing the dorsal mantle fold (*Md*); the anterior and posterior mantle furrows; the union between the two halves of the peduncular coelom.

#### PLATE VI.

- Fig. 31. Lateral view of a larva of the same stage as the preceding, showing anterior and posterior mantle folds (*Fa* and *Fp*), apical and ventral sense plates (*CG* and *SG*), enteron and coelom.
- Fig. 32. Dorsal view of older larva, showing increased prominence of mantle and deep constriction of anterior mantle furrow.
- Fig. 33. Dorsal view of an older larva, showing the mantle in process of growing back over the peduncle; the coelom is almost entirely confined to the mantle.
- Fig. 34. Dorsal view of one of the oldest free-swimming larvæ; the mantle has almost entirely covered the peduncle.
- Fig. 35. Lateral view of a larva of the same stage as the preceding, showing apical and ventral sense plates (*CG* and *SG*), dorso-ventral extension of enteron and greater width of mantle chamber on dorsal side.
- Fig. 36. Optical section in longitudinal frontal plane of a larva of the same stage as the preceding, showing apical sense plate and cerebral ganglion; mantle chamber and setæ sacs; cephalic, peduncular and mantle coelom (*Cc*, *Cp*, *Cm*).

#### PLATE VII.

- Fig. 37. Section of an embryo of the stage shown in Fig. 13, showing dark staining granules in the outer ends of the cells and yolk spherules in the blastocoel.
- Fig. 38. Section of an embryo of the stage shown in Fig. 14.
- Figs. 39-42. Four transverse sections of an embryo of the stage shown in Fig. 20; Fig. 39 being the most posterior and Fig. 42 the most anterior section drawn.
- Figs. 42a and 42b. Longitudinal sections through an embryo of about the same stage as is shown in Figs. 39-42, showing the formation of the septum which separates the enteron from the enterocoel.

#### PLATE VIII.

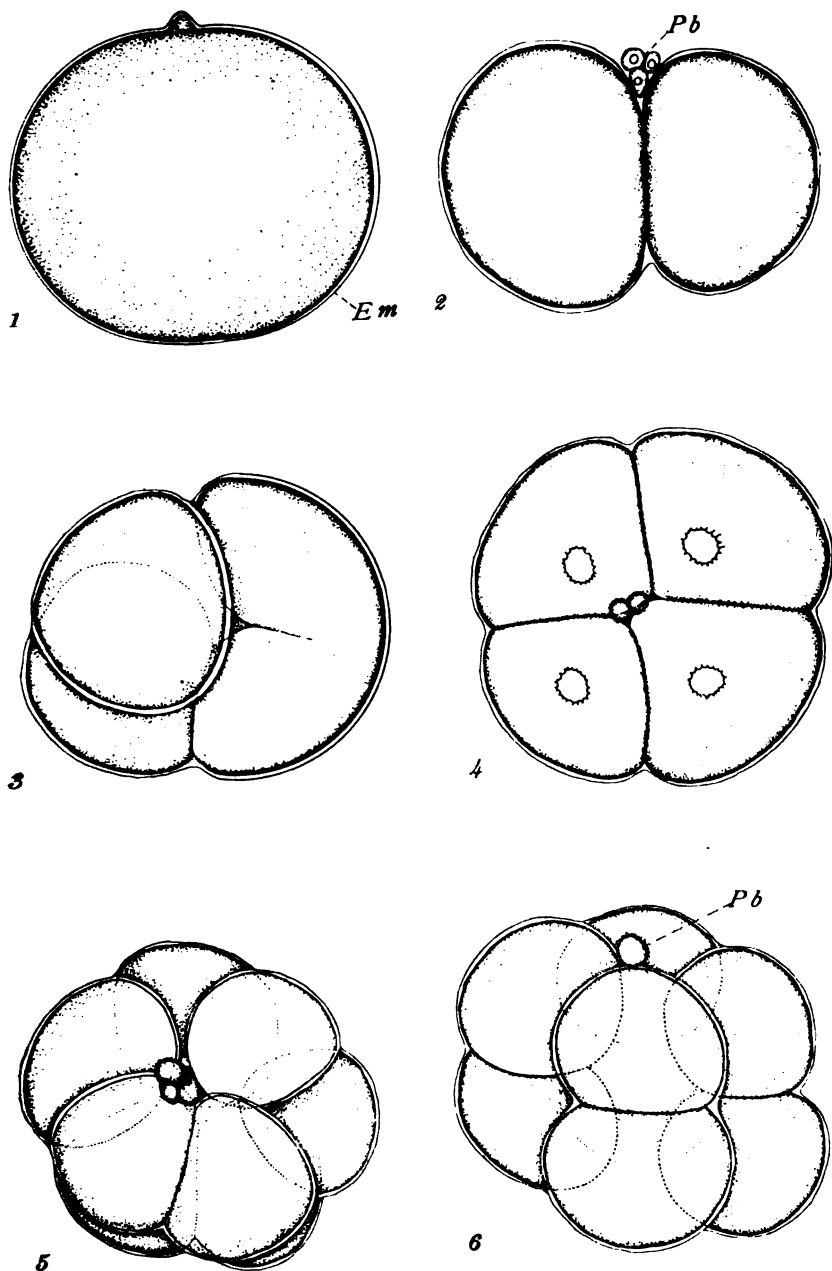
- Figs. 43-47. Five transverse sections of a larva of the stage shown in Fig. 24; Fig. 43 being the most anterior and Fig. 47 the most posterior section drawn.
- Figs. 48-52. Five transverse sections of a larva of the stage shown in Fig. 29; Fig. 48 being the most anterior and Fig. 52 the most posterior section drawn.

## PLATE IX.

- Figs. 53-55. Three oblique sections from the dorsal anterior (*DA*) to the ventral posterior (*VP*) region of a larva of the stage shown in Fig. 31 (the sections are nearly in the plane of the reference line from *E* in Fig. 31).
- Figs. 56, 57. Two longitudinal frontal sections of a larva of the same stage as the preceding, Fig. 56 being ventral to Fig. 57.
- Fig. 58. Longitudinal sagittal section of a larva of the same stage as the preceding; the section passes through both the apical and the ventral sense plates (*CG* and *SG*).

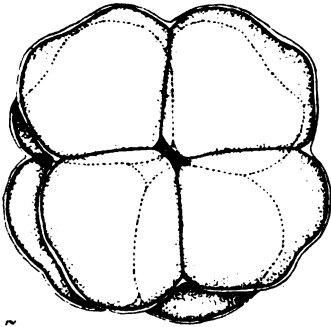
## PLATE X.

- Figs. 59-64. Six transverse sections of a larva of the stage shown in Figs. 34-36; Fig. 59 being the most anterior and Fig. 64 the most posterior section drawn. Fig. 59 passes through the cephalic region; Fig. 60 lies just behind the anterior mantle furrow; Figs. 61-64 are through the mantle and peduncle.

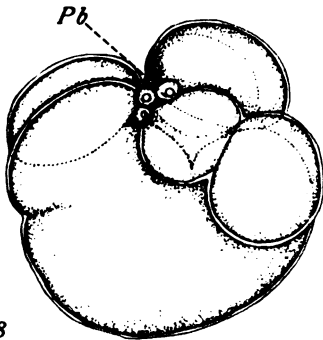




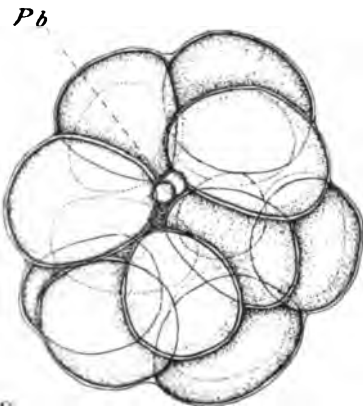




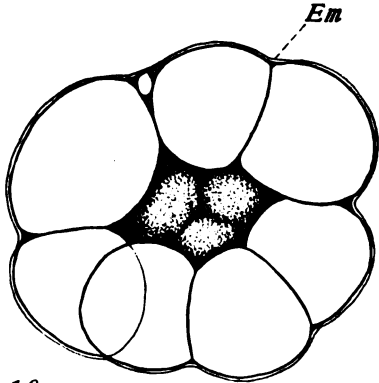
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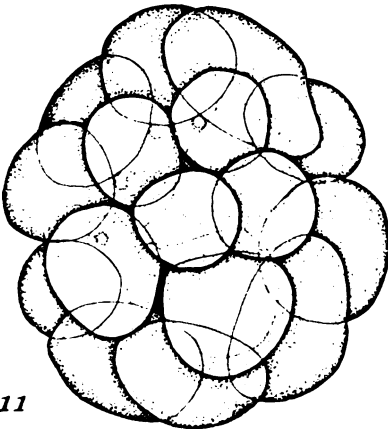
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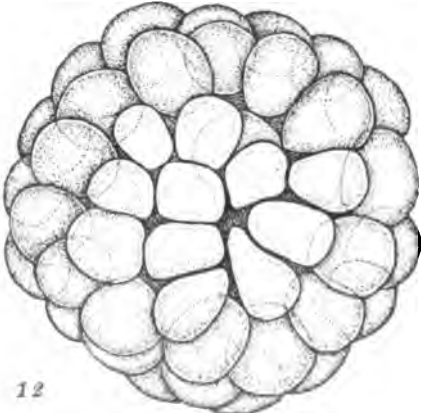
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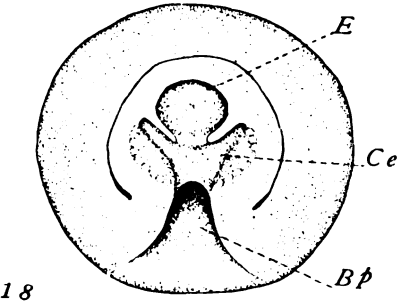
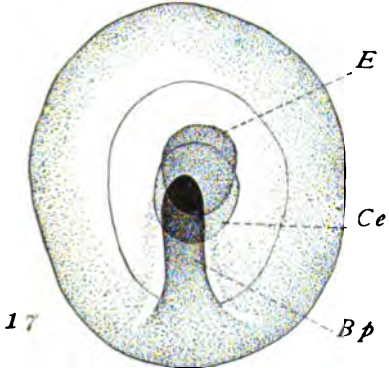
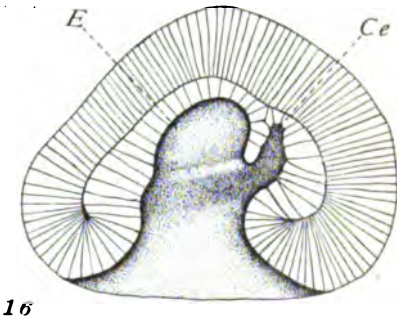
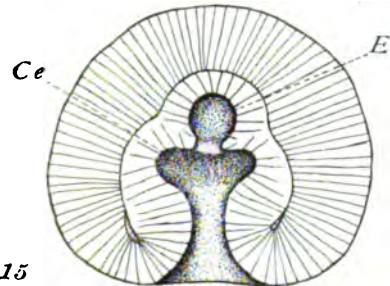
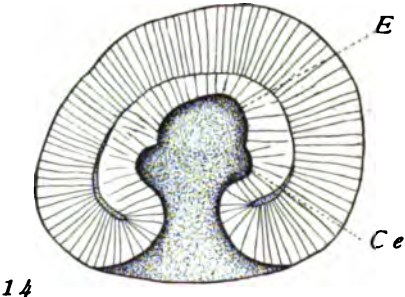
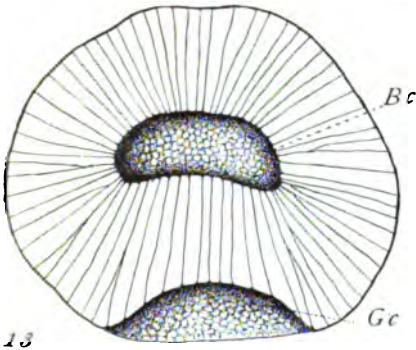


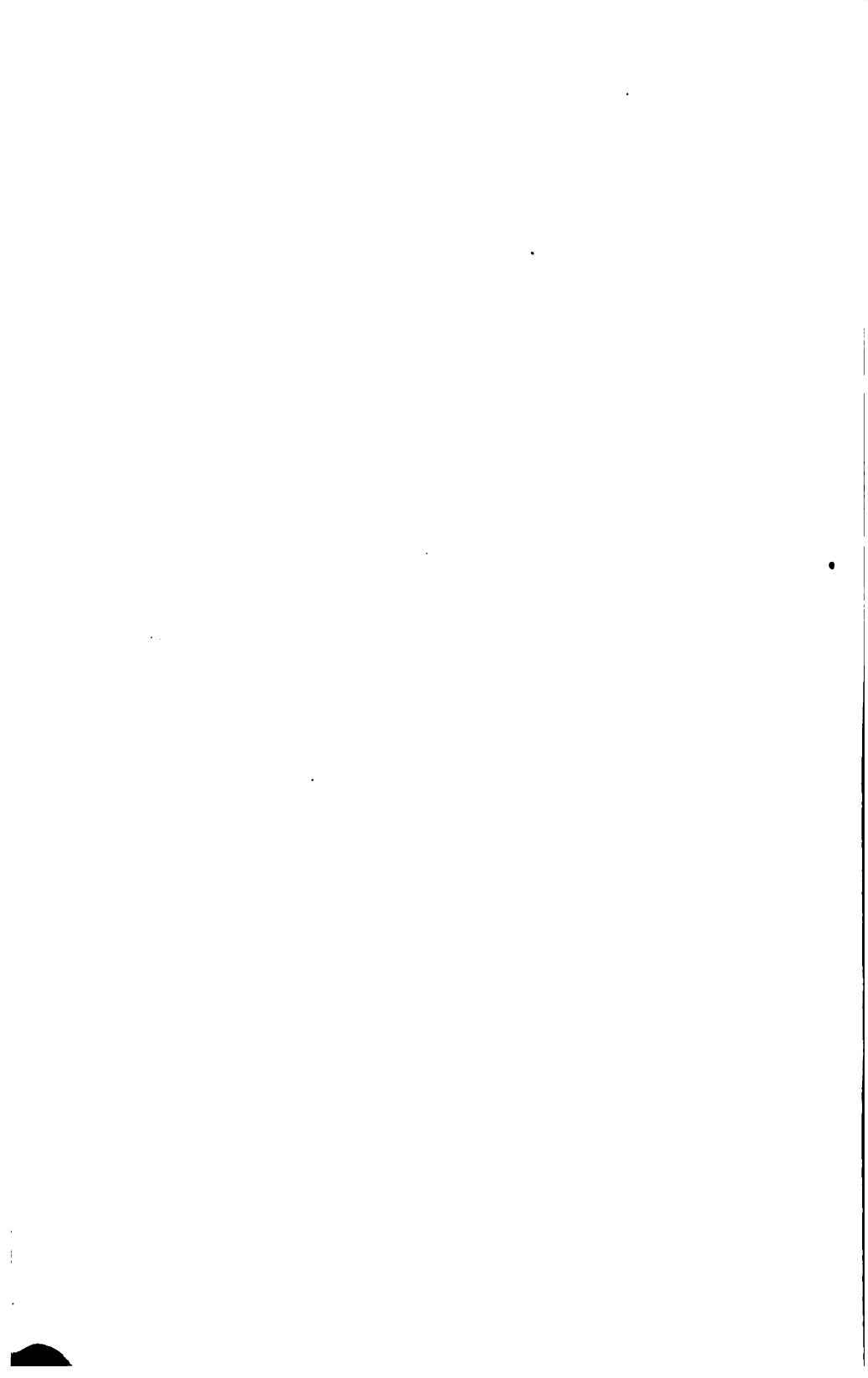
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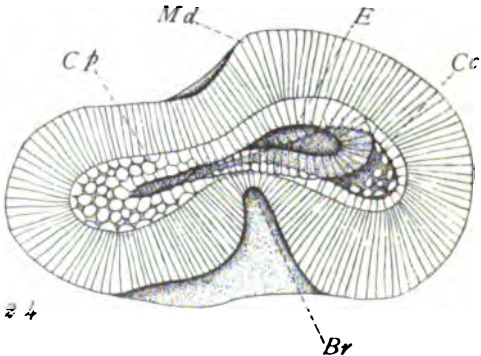
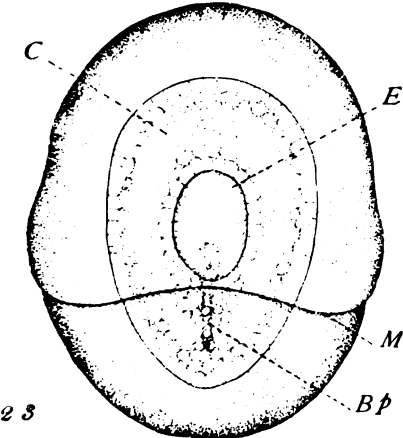
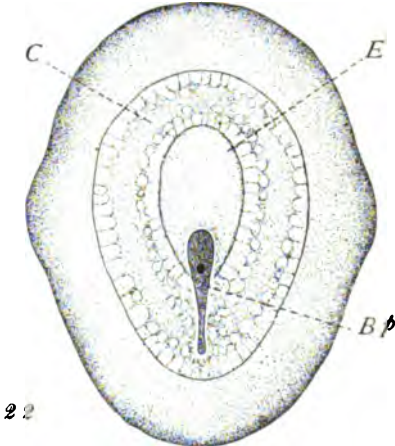
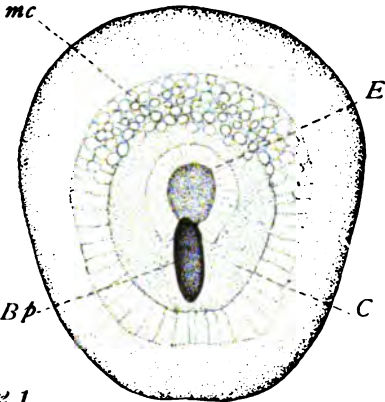
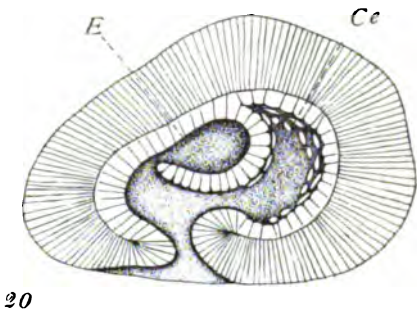
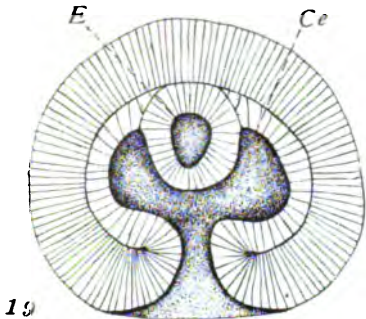


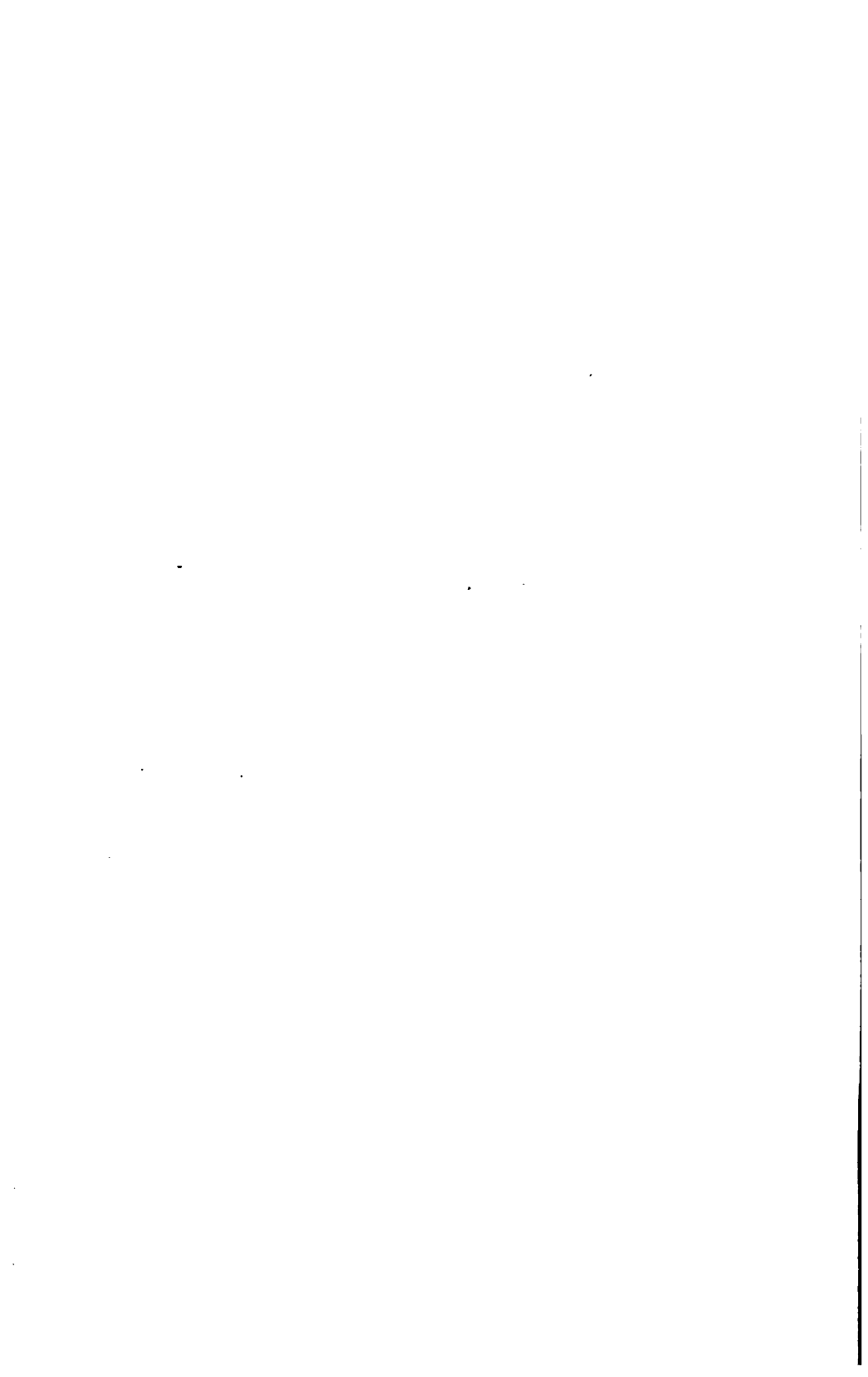
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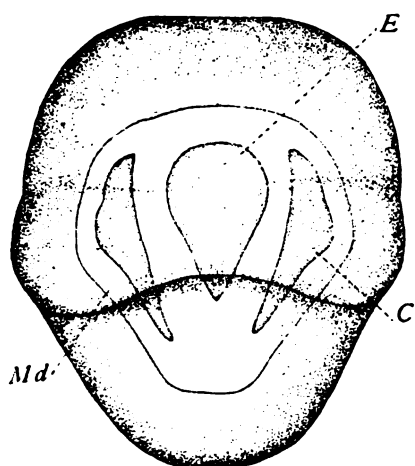




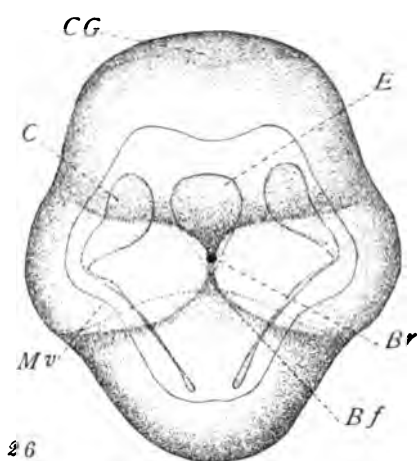




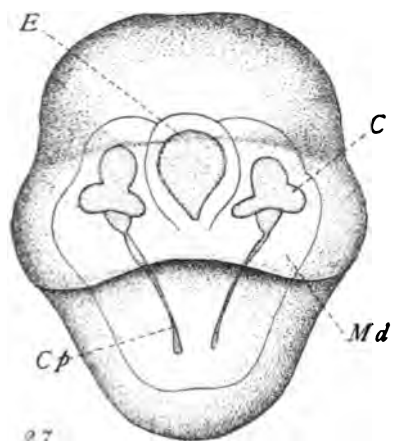




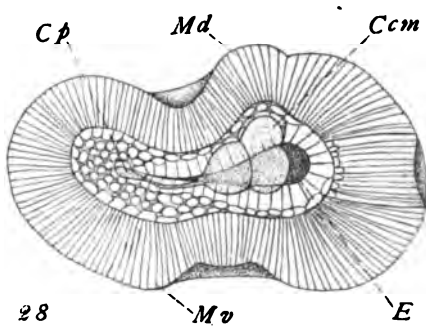
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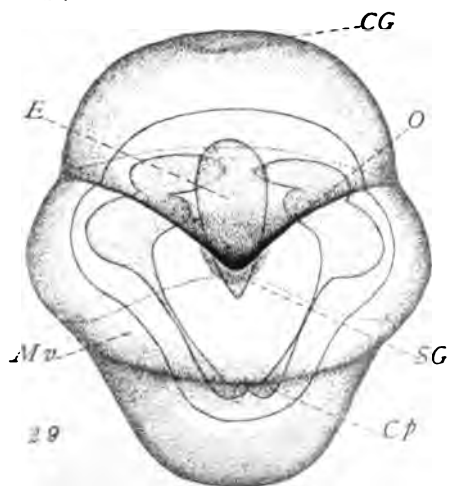
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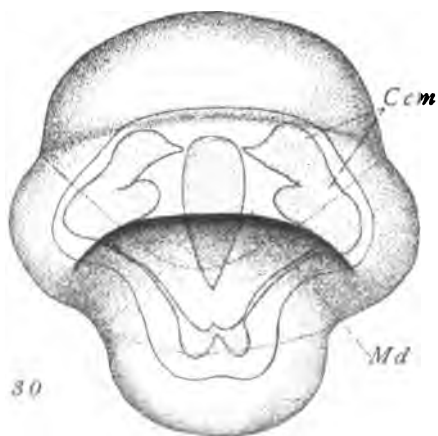
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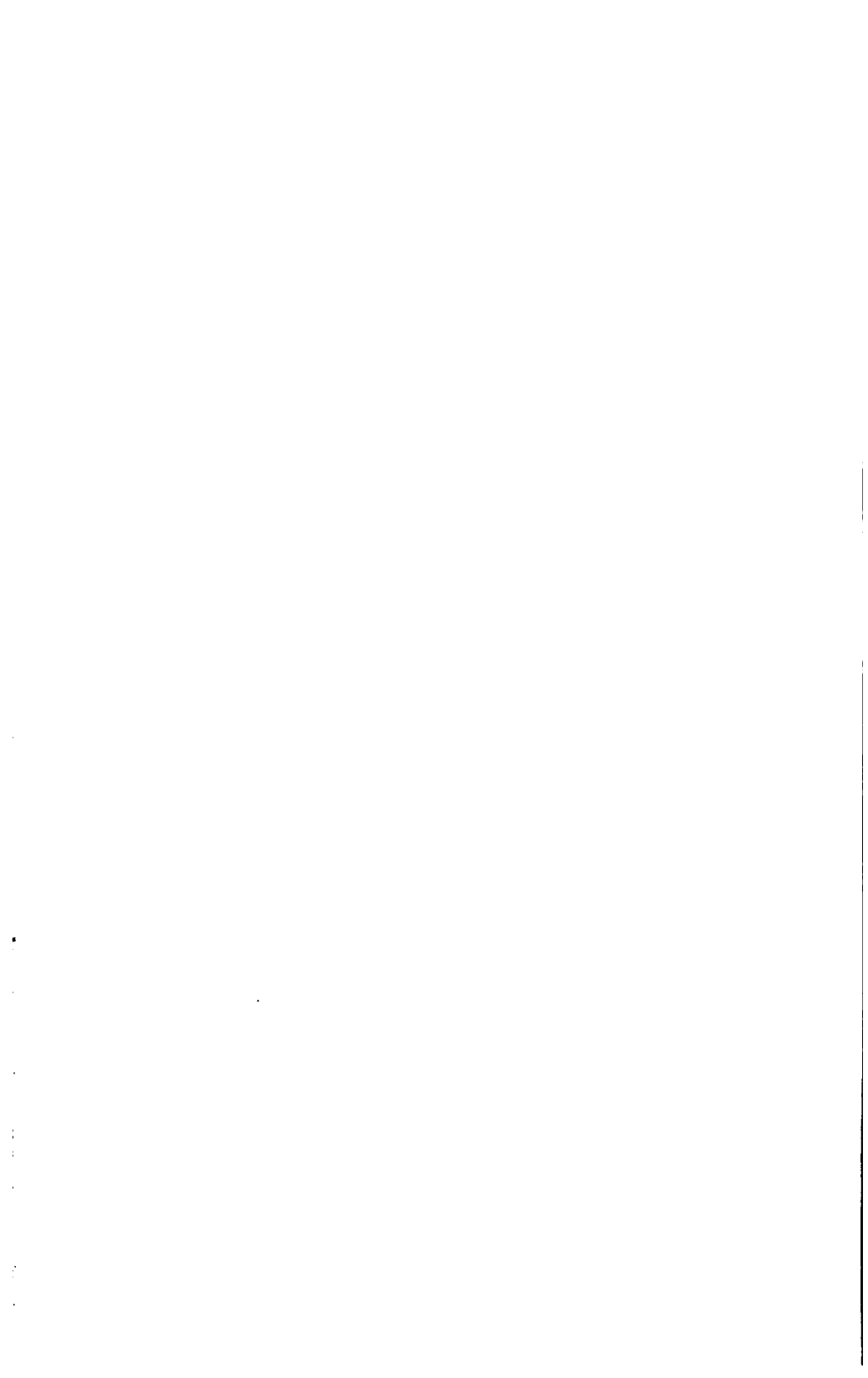


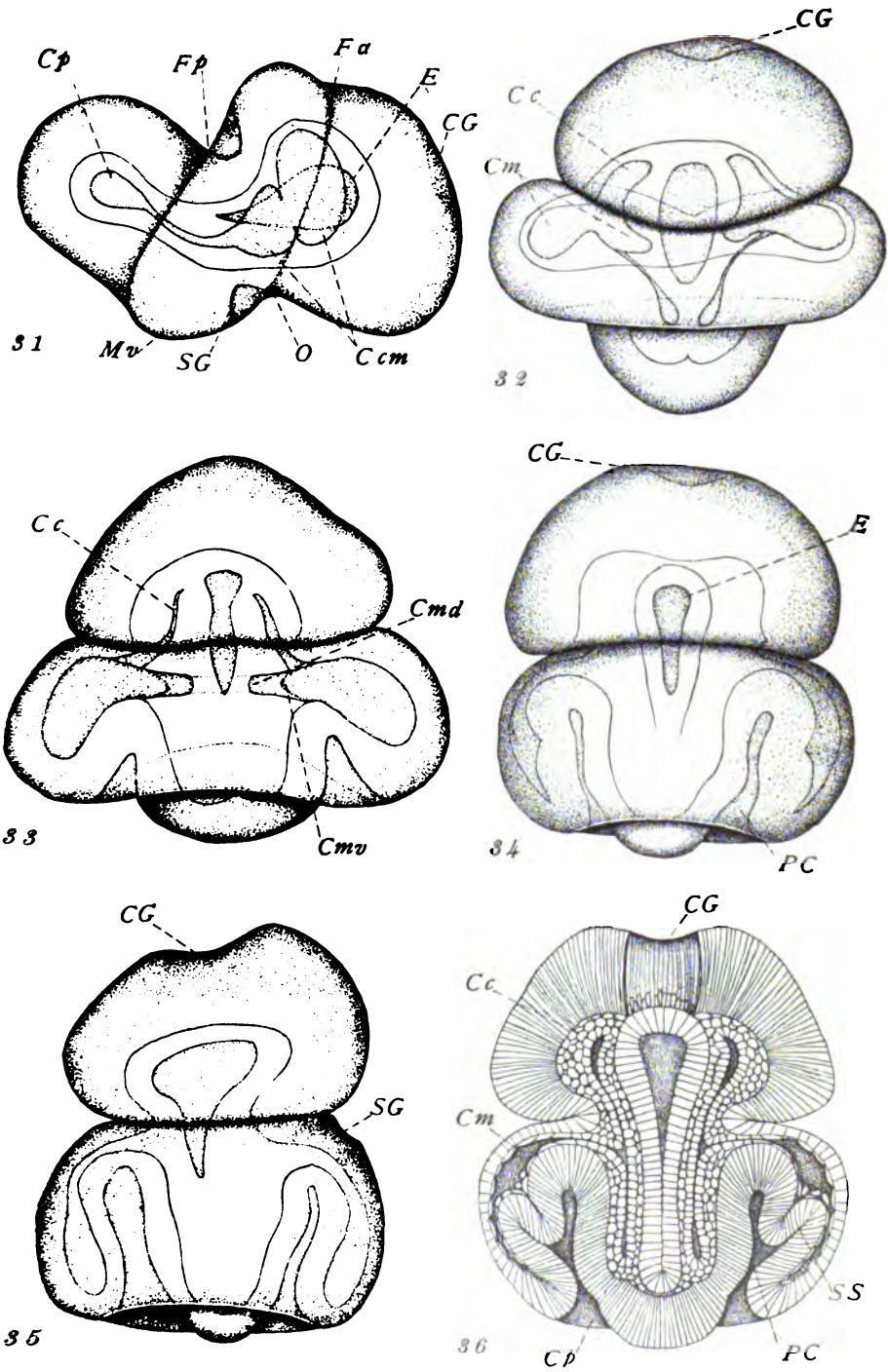
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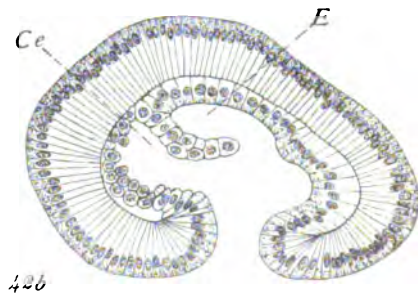
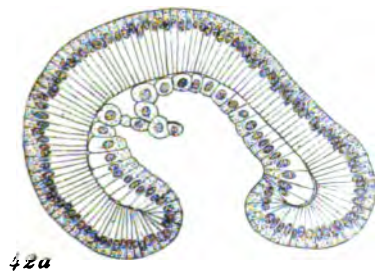
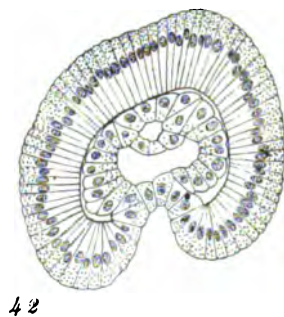
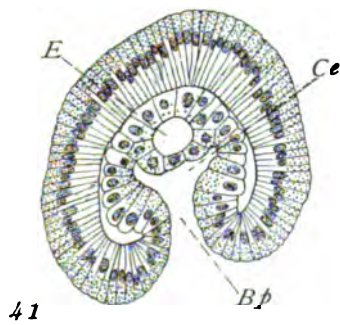
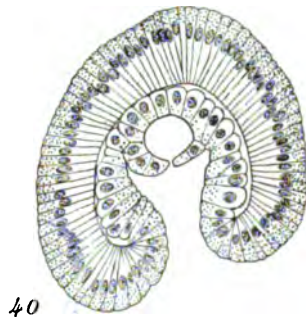
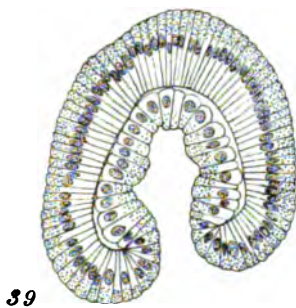
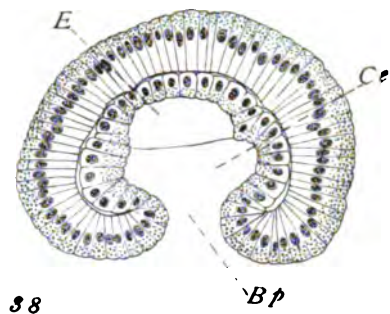
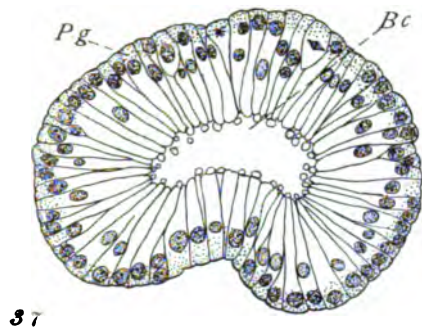




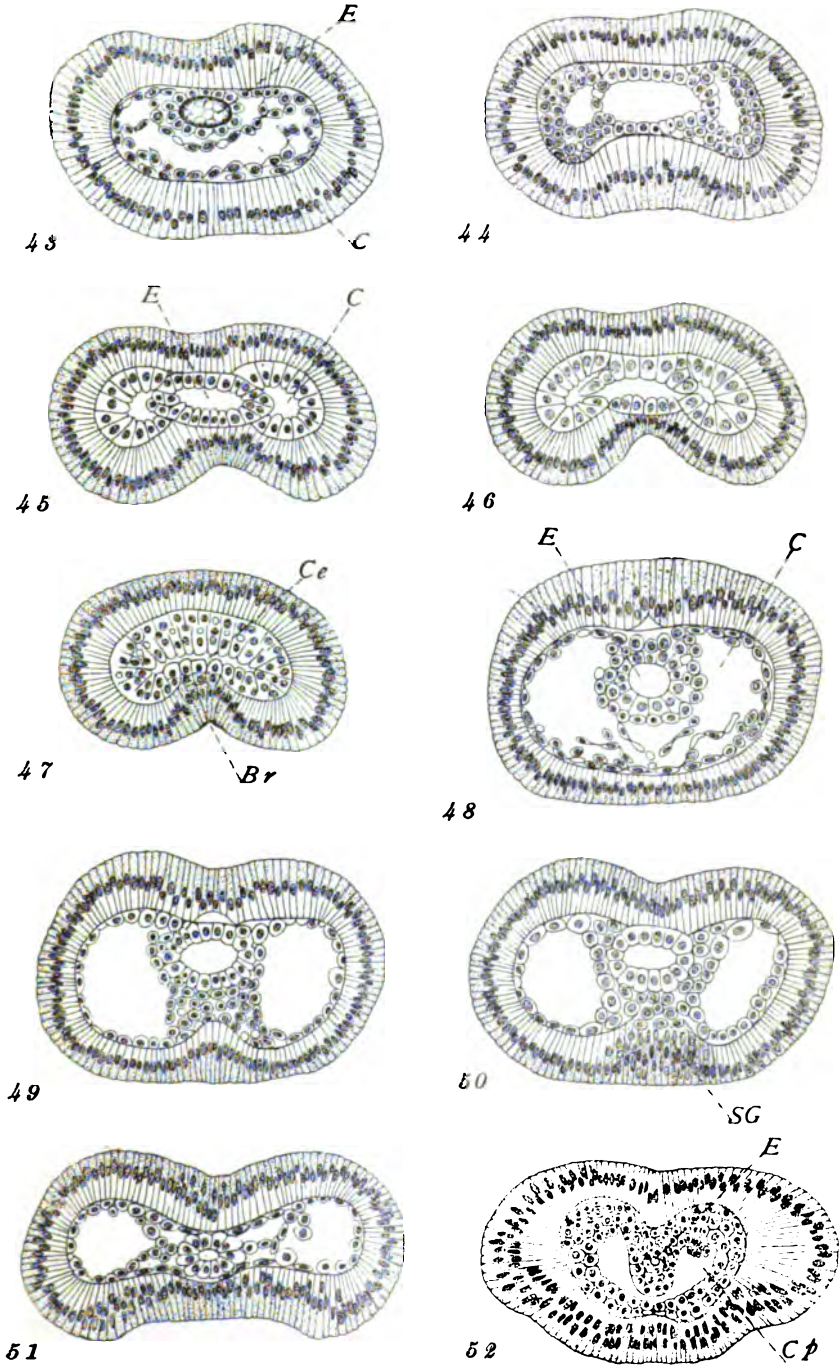


CONKLIN ON TEREBRATULINA SEPTENTRIONALIS.





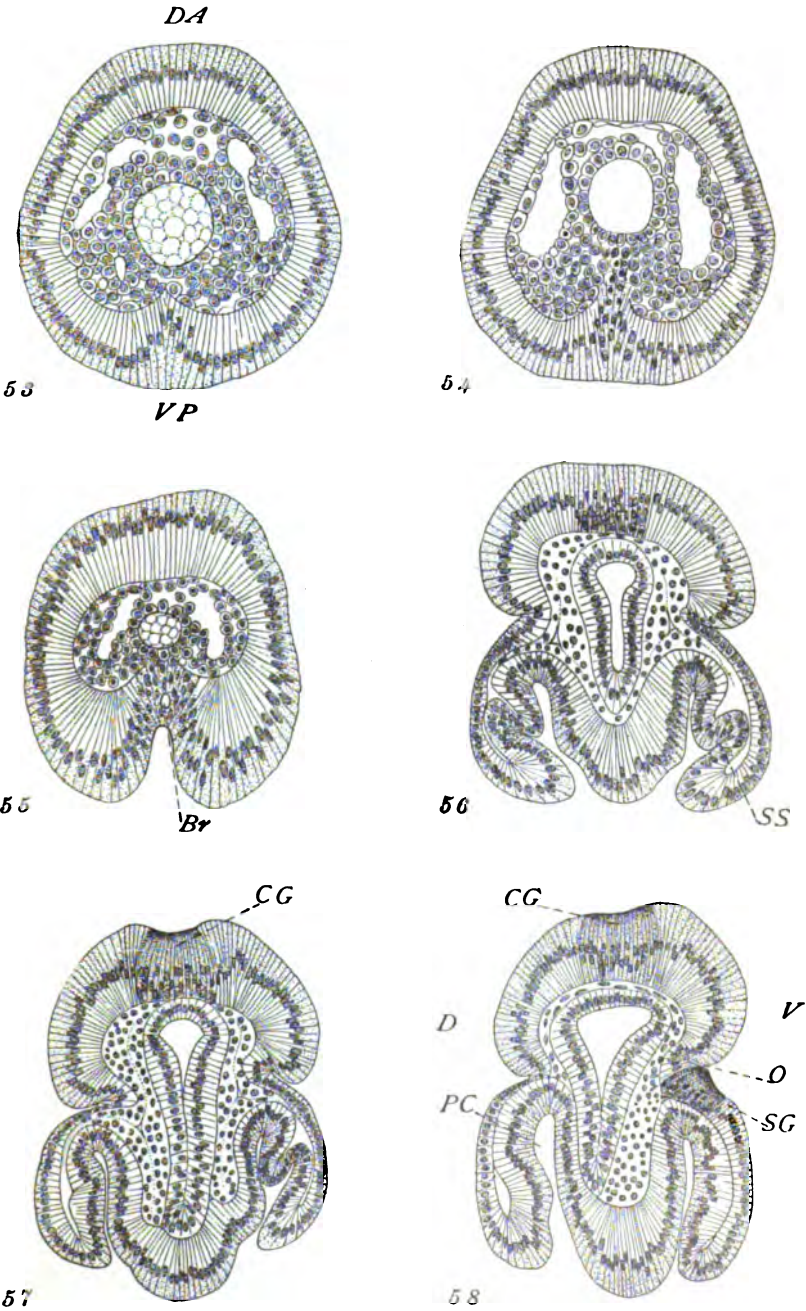




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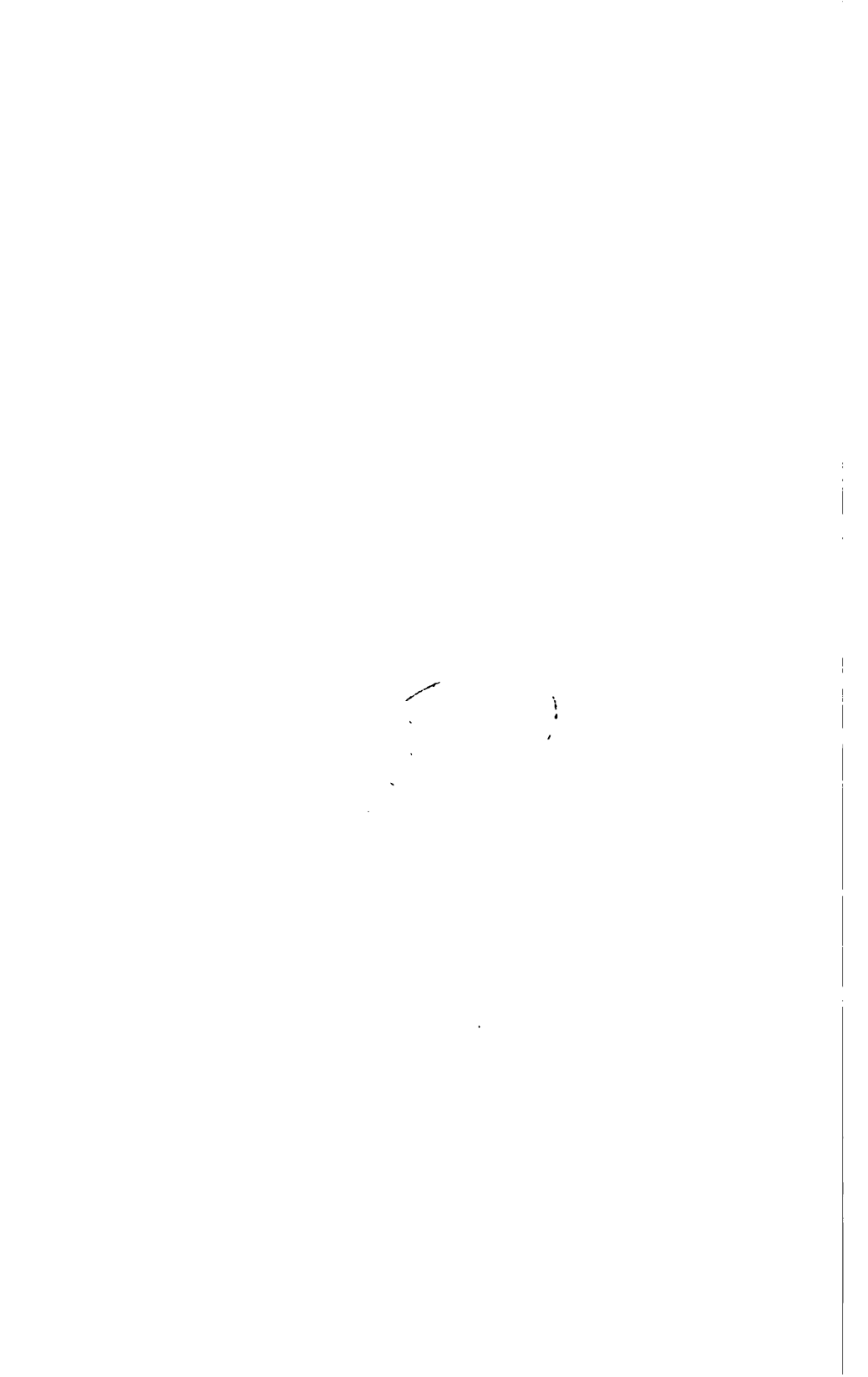


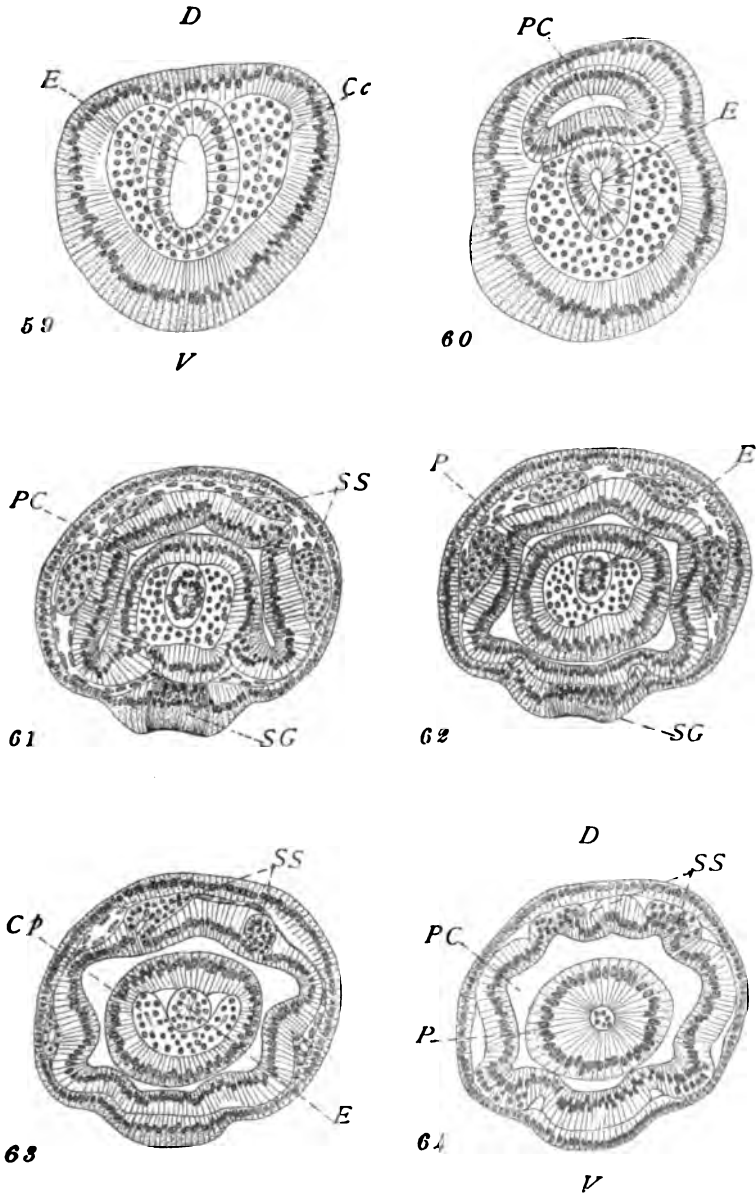




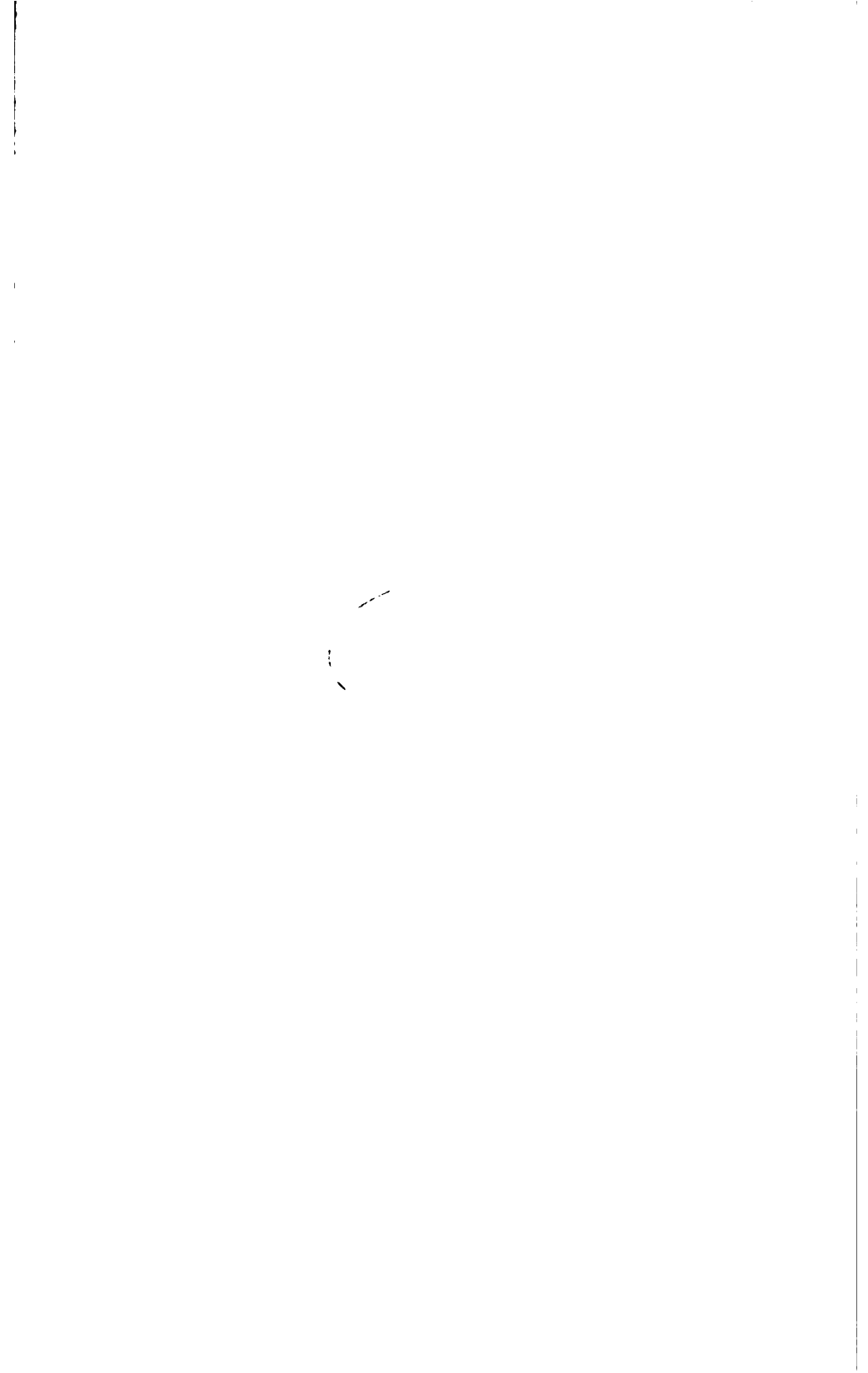
CONKLIN ON TEREBRATULINA SEPTENTRIONALIS.







CONKLIN ON TEREBRATULINA SEPTENTRIONALIS.



THE SPERMATOGENESIS OF ONISCUS ASELLUS LINN.<sup>1</sup>  
WITH ESPECIAL REFERENCE TO THE  
HISTORY OF THE CHROMATIN.<sup>2</sup>

BY M. LOUISE NICHOLS.

(Plates XI-XVIII.)

(Read April 4, 1902.)

This study was begun in the month of February, 1899, in order to ascertain the mode of origin of the peculiar spermatozoa of the land Isopods. I have now completed, so far as I am able at the present time, the investigation undertaken for that purpose. Before entering, however, upon a description of my observations, I wish, at the close of a work which has proved both interesting and instructive, to express my gratitude to my instructors, Prof. E. G. Conklin and Prof. Thomas H. Montgomery, Jr., for the inspiration and the many valuable suggestions which have aided me toward its completion. To the latter I am particularly indebted for his helpful criticism concerning the earlier stages of the spermatogenesis.

METHODS.

The material was fixed either in Flemming's fluid, Hermann's fluid or in Gilson's fluid (acetic-nitric sublimate). It was stained for the most part with iron hæmatoxylin, but for purposes of comparison also with saffranin and malachite green (Wilcox) (1895), saffranin and gentian violet, Delafield's hæmatoxylin and Bordeaux red, and with the Biondi-Ehrlich triple stain. The study of the spermatozoa was also pursued by teasing apart the vas deferens with needles, staining the fresh material with hæmatoxylin or with acetic-methyl green, and mounting in glycerin. Permanent mounts were also made of fixed and stained material. I consider Wilcox's double stain with saffranin and malachite green to be a valuable one, for the reason that it can be used with good effect on material fixed in Flemming's fluid. It gives in reality a triple stain, for in successful preparations the cytoplasmic structures stain green, active chromatin, centrosomes and true nucleoli red, while resting chromatin takes a purple color. Its chief disadvantage is that it will in time fade.

<sup>1</sup> The species was determined by means of the works of Budde-Lund (1885) and of Richardson (1900). The species is also known as *O. murarius*, Cuv.

<sup>2</sup> A thesis for the degree of Ph.D. at the University of Pennsylvania.

## I. STRUCTURE OF THE MALE REPRODUCTIVE ORGANS.

The male reproductive organs of the land Isopods are paired and lie on either side of the tubular intestine, occupying almost the entire length of the thoracic region.

The testis consists of three narrow lobes, which are attached to the body musculature by slight strands of tissue. These lobes are distinct from each other and open successively into the anterior expanded portion of the vas deferens (Fig. 1). Posteriorly the vas deferens narrows to a more slender tube, which joins its fellow of the opposite side and opens through the penis, which is unpaired and is said by Gerstaecker (1882) to be an outgrowth from the seventh thoracic segment. It is enclosed by the modified internal lamellæ of the first abdominal appendages (Fig. 1).

Sections of the vas deferens (Fig. 3) show its expanded portion to be lined with cells of large size, which possess prominent spherical nuclei. The nucleus is sometimes surrounded by a clear space, varying somewhat in size. The chromatin is in the form of closely crowded granules. Between these are sometimes other granules, which with the iron hæmatoxylin stain are less deeply colored, and with Bordeaux red and Delafield's hæmatoxylin take a red tint. The periphery of the latter is usually darker in color. The surrounding cytoplasm is filled with particles of a rounded shape, which take cytoplasmic stains (Fig. 4a). In one preparation the cytoplasm of these cells was filled with particles, not rounded in shape but thread-like, and taking a very dark stain with iron hæmatoxylin. The chromatin consisted of granules of varying size, which appeared lighter in the centre and possessed a darker margin (Fig. 4b). I do not know whether there is any connection between the particles within the nucleus and those without; the subject might possibly repay further research. The appearance of these cells suggests strongly that they have a secretory function; no doubt the fluid which bathes the spermatozoa is produced by them. They are more abundant at those places where the follicles open into the vas deferens and grow more scarce in the region where the narrow portion of the vas commences (Fig. 3). Between them are to be seen nuclei of smaller size, whose chromatin is not so distinctly and regularly granular. These lie in a cytoplasmic reticulum of a coarse mesh, without well-defined cell boundaries and containing no granules. This tissue apparently forms a supporting

membrane for the secretory cells. It is continuous with the layer of cells which line the narrow portion of the vas deferens and is similar to it in structure (Fig. 3). The narrow portion of the vas, as a rule, is covered externally by dark pigment, thus forming a marked contrast in the fresh state to the milk-white walls of the anterior portion (Fig. 1). Between the pigment layer and the lining cells, delicate muscle-fibres are occasionally discernible.

The three lobes of the testis are seen in section to be three follicles (Fig. 2). Each follicle is covered by a thin membrane which is provided with delicate muscle-fibres (Fig. 5*m*, *l*). The margins of the follicle are occupied by large nuclei of unsymmetrical outline, containing irregular blocks of chromatin interspersed with finer granules. Cell boundaries between these nuclei are not visible. They can sometimes be seen to be undergoing amitotic division, of a character similar to that described by vom Rath (1891) for *Astacus* (Fig. 5*f*, *c*). In follicles of a certain stage of development these nuclei, as will be explained later, are subject to degeneration.

The strands of tissue, by means of which the follicles are suspended from the body wall, are made up of cells which also divide amitotically and which are similar in appearance to the follicle nuclei, inasmuch as their outlines are irregular, but the blocks of chromatin are of larger size and the nuclei are separated from each other by distinct cell walls (Fig. 6).

The interior of the follicle, except during the migration of the follicle cells, is occupied entirely by the germ cells, which are in differing stages of development in the three follicles of one side. Corresponding follicles of opposite sides of the body contain, however, germ cells which have developed to very nearly the same degree.

Fig. 2 shows, in a typical case, the comparative degrees of development to which the cells of the three follicles have attained. Each follicle may be divided into two principal regions of growth, composed of cells of different generations and of different degrees of development. Thus, in the most posterior of the follicles (*a*), the apical third is occupied exclusively by spermatogonia, some of which can be seen in mitosis; the basal region, on the other hand, by spermatids in a not very advanced stage. Follicle cells occur on the outside of the follicle, being especially abundant in the basal region. In the adjacent follicle (*b*), the apical two-thirds is occupied by cells in the synapsis stage, the remaining portion by sper-

matids in a stage of development later than that of follicle (*a*). Along the margin of the follicle are found scattered small groups of spermatogonia (Fig. 2, *spg*). The third and most anterior follicle (*c*) contains chiefly spermatocytes in a late prophase. Groups of spermatogonia similar to those of follicle (*b*) are here also found scattered along the margin and nearly filling the extreme apical portion. The follicle cells in the basal region are undergoing not only active amitotic division, but to a certain extent degeneration (Fig. 5). Their active multiplication or fragmentation causes them to crowd in toward the axis of the follicle.

From a comparison of the extent of these growth regions in the three follicles, the developmental cycle may be conceived somewhat as follows. The spermatozoa, when fully formed, are forced into the vas deferens. Since they have no motion of their own, this is probably caused by the contraction of the muscle layer of the follicle, perhaps assisted by the pressure of the growing cells in the apical region. During this process, the spermatogonia in the apical portion of the follicle divide and come to fill the space left vacant by the discharged sperm. The rate at which this replacement takes place and the comparative development of the cells in the two regions may vary in different follicles, for I have preparations in which few or no spermatozoa are seen—in other words, most of them had probably been discharged, and at the same time the replacing spermatogonia are scattered and few in number. In others, as is shown in the diagram (Fig. 2*a*), the spermatozoa, in an early stage of development, occupy the basal portion of the follicle, while the apical portion is packed with spermatogonia. The majority of the spermatogonia thus filling up the follicle proceed in their development, while the remainder form the groups of cells along the margin of the follicle already described in follicles (*b*) and (*c*), and which are destined later to again supply a new generation of cells. The spermatids also proceed in development and are forced into the vas deferens. A condition like that represented in diagram (*b*) (Fig. 2) thus arises—the basal region filled with spermatozoa in a late stage about to pass into the vas deferens and the apical region with cells which have progressed as far as the synapsis stage. Later, the spermatozoa having been completely discharged, the cells of the apical region come to occupy the basal part of the follicle, being now less compactly pressed together (Fig. 2*c*). Their development progresses until, having become mature spermatozoa, they pass into

the vas deferens, the spermatogonia again fill the apical region, and the cycle is repeated.

The invasion of the follicle cells begins, as a rule, when the germ cells are in an advanced prophase and may continue later. Many of the germ cells likewise degenerate, and they, together with the follicle cells, form a disintegrated mass in which the spermatids lie. In young follicles, which have not as yet matured sperm, the basal region is filled with follicle cells, the apical region with spermatogonia. This is sometimes true also of older follicles which have recently discharged the sperm.

It will thus be seen that a series of stages, illustrating the complete history of the changes through which the germ cell pass, can be obtained only by an examination of numerous testes. Duplicates are often obtained and some of the stages occur very infrequently, probably owing to a greater rapidity of development at certain periods.

This study was begun in the latter part of February. In March or April, according to the rigor of the weather, the land Isopods in the vicinity of Philadelphia commence to breed. The breeding season continues during the summer months. There are, in a single year, several cycles of development of the reproductive elements; the exact number I have not determined. It is therefore possible, at almost any time of year, by examination of a sufficient number of individuals, to procure a complete series of developmental stages.

## II. SPERMATOGENESIS.

### 1. *Spermatogonia.*

The resting spermatogonia are distinguished from the follicle cells by their smaller size, the distinctness of the cell walls, and by the fact that in their nuclei the chromatin masses are of smaller size and show indications of an arrangement into a network (Fig. 11a). They possess a prominent true nucleolus of more or less rounded form. Some cells contain one or more smaller nucleoli.

It is impossible to determine the exact number of spermatogonic divisions. They are probably numerous, since it must require a considerable number of divisions of the spermatogonia remaining in the follicles to fill the space left vacant by the discharged sperm. The cells vary somewhat in size. When the apical region of the follicle is filled with spermatogonia the individual cells are small, but when the follicle is not well filled and the spermatogonia are



beginning the task of producing a new generation, individual cells often equal the spermatocytes in size (Figs. 10 and 13). In the cytoplasm are occasionally seen irregular masses of a dull brown tint (yolk?), but neither sphere substance nor centrosomes are apparent in the resting cell.

In nuclei preparing to divide, the chromatin is seen to be arranged in the form of slender, elongated threads, which, so far as I have been able to discover, in no case form a continuous spireme (Fig. 7). In the cytoplasm surrounding a nucleus of this character are visible two minute black specks joined by a delicate thread, presumably the centrosome undergoing division. The nuclear membrane at this stage begins to fade. Figs. 8, 9 and 10 show stages immediately succeeding the stage shown in Fig. 7. The threads have become shorter and thicker, the nuclear membrane has entirely disappeared, and the centrosomes have become more widely separated. The amount of segmentation of the thread varies in different cells. In Fig. 11*b* is shown a nucleus in which very little segmentation has taken place, although the thread is considerably thicker than that shown in Fig. 7. The linin threads joining the chromosomes are of extreme delicacy and difficult to discover. Occasionally, however, (Fig. 9) fine fibres may be seen stretching from one chromatin thread to the next. The shortened and thickened chromosomes then arrange themselves into an equatorial plate (Fig. 12). The appearance of the plate, both in side and in pole view, is irregular. The division of the chromosome into chromomeres and their longitudinal division is visible only in very thin sections, which have been stained with iron hæmatoxylin and rather strongly decolorized (Fig. 14). The centrosomes and spindle-fibres of the spermatogonic, mitotic figure are not quite so prominent as those of the spermatocytic divisions. The same is true of the polar radiations. Central spindle-fibres are apparently entirely lacking. After splitting of the chromosomes the halves diverge, in the manner of the two legs of a pair of compasses, the divergence commencing at one end, while at the other end the two halves remain in contact (Fig. 15).

A still later anaphase is shown in Fig. 17. The chromosomes have become massed together, the spindle-fibres are beginning to disappear and the centrosomes are almost lost to sight. The constriction of the cell body, observable to a slight degree at this stage, becomes more marked and a membrane comes to separate the two daughter cells (Fig. 19).

The reconstruction of the nucleus consists of the breaking up of the chromosomes into fine granules, which are connected by linin threads of great delicacy, and in the development of a nuclear membrane (Figs. 19, 20, 21). The change in chemical composition of the chromatin is indicated in sections stained with safranin and gentian violet by a gradual change in color from red to blue. As the cell body constricts slight thickenings are discoverable on the connective spindle-fibres in the equator (Fig. 18), which, as the constriction proceeds, grow fewer in number and more conspicuous in size until they are finally reduced to a single large swelling, from which radiate the spindle-fibres, by this time grown faint (Fig. 19). At a stage a little later than the one just described I have occasionally seen a small black body wedged in the angle between the daughter cells (Fig. 20). Its appearance is similar to the "Flemmingscher Körper" described by Hoffmann (1898) for *Limax maximus* (see his Figs. 31, 32, 33) and strikingly like that of the rabbit described by von Winiwarter (1900, Figs. 9 and 10).

## 2. Growth Period.

The anaphase of the last spermatogonic division is decidedly different from that just described. The chromatin threads lie massed together and entangled near the centre of the cell (synapsis). They are surrounded by a clear space bridged over by slender acromatic fibres, which connect the chromatin threads with a narrow layer of cytoplasm lying close to the cell wall. No trace of centrosome or sphere substance (idiozome) is discoverable (Fig. 22). The chromosomes now spread apart, although still connected by strands of linin. They are seen to be for the most part V-shaped. The chromatin granules are rather irregularly distributed, being frequently massed together in lumps (Fig. 24).

In a thin section of a cell at a stage slightly later than this there appeared a minute black dot, surrounded by a vaguely defined area, slightly more dense than the rest of the cytoplasm (Fig. 23). I hesitate to attach importance to this, as it occurred in very few cases.

The threads now elongate, and during this process the granules of which they are made up divide, so that the thread becomes longitudinally split. The granules apparently do not divide simultaneously. Even in the same thread some of them show division, while others remain entire (Fig. 25). The split is to be seen with

the greatest clearness in sections stained with iron hæmatoxylin and strongly decolorized. The chromosomes are very irregularly distributed, only occasionally a part of them, six or seven, may be grouped with reference to a central point. Of the entire number of chromosomes present it is difficult to be certain, owing to the fact that they overlies each other so closely. The number, however, is certainly less than that present in the spermatogonia and not greater than sixteen (Fig. 26). The reduction in the number of chromosomes, therefore, apparently takes place at this stage, and the V-shape so prevalent is due to the approximation of two chromosomes to form a single bivalent one. The place of union is frequently covered by chromatin, but a connection of linin can sometimes be discovered (Fig. 27). This figure also shows the varying angle at which the univalent chromosomes may approach each other. Occasionally they may even form a complete ring.

The threads become more and more attenuated (Fig. 28), and finally by anastomosis are transferred into the nuclear reticulum of the resting spermatocyte (Fig. 30). During the elongation of the chromosomes the chromatin granules divide and redivide (Figs. 23-28), so that they become very numerous, and as the elongation progresses the longitudinal split becomes less easily discoverable, until in the resting cell it can no longer be made out. Cells are sometimes seen in which, just before the formation of the nuclear membrane, the network lies to one side, being connected by slight strands of linin with the surrounding cytoplasm (Fig. 31).

The fact that the chromosomes remain distinct until just before the formation of the nuclear membrane points to a maintenance of their individuality in the resting cell.

The nuclear membrane appears to form as a condensation of achromatic substance, upon which later appear granules staining deep blue with hæmatoxylin (Fig. 29).

A peculiar fact with reference to the last spermatogonic division has struck my attention and I have been unable to explain it very satisfactorily. It will be seen from Fig. 2 that nearly all the cells in the apical portion of follicle (*b*) are in the synapsis stage. It might be supposed from this that sections would be obtained of follicles filled apically with the spindles of the last spermatogonic division. Such a condition, however, I have never found, although I have examined a large number of testes at different seasons of the

year. The karyokinetic figures of the spermatogonia are always scattered and it is impossible to distinguish between the early and late ones.

### 3. *The Maturation Divisions.*

In preparing for the first maturation division the meshes of the nuclear network become coarser, the granules more distinct and aggregated into separate threads, joined together by linin (Figs. 32-36). The manner of their origin again lends support to the view concerning their individuality in the resting cell. A still greater condensation of the granules leads to a shortening and thickening of the chromosomes (Figs. 37 and 38), the final result of which is the production of sixteen compact masses of chromatin, still connected by linin threads (Fig. 44). Condensation does not proceed at an equal rate in all the chromosomes of a nucleus. Fig. 45*a* shows a small portion of a nucleus in which lie side by side two chromosomes, in one of which the final dumbbell-shape is almost completed, while in the other the condensation of the chromatin is but little advanced. These sixteen masses are of various forms. Some are dumbbell-shaped, two spheres of chromatin joined by linin; some are crescent-shaped and still others are more or less complete rings (Figs. 39-45). The different forms may occur in the same nucleus, but apparently without constancy in the ratio of relative frequency of occurrence. The dumbbell-shape, straight or slightly curved, is abundant, some cells containing no complete rings (Fig. 41). Other cells contain a comparatively large number of rings or crescents (Figs. 39 and 40).

Two main types may be distinguished among the chromosomes according to their structure and mode of origin—*i.e.*, (1) those in which the bivalent chromosome consists of two univalent chromosomes lying end to end, as in those having the dumbbell-shape, and (2) those in which the univalent chromosomes lie side by side, as in those arising through a ring or narrow V-shape. A form intermediate between these is represented by those having a crescent-shape. The different types and their probable mode of origin are shown in the diagram (Fig. 68*a, b, c*). It is interesting to note that these types can be distinguished in the synapsis stage (Fig. 27), although they are here not so well marked as in the prophase of the first maturation division.

In cells stained with iron hæmatoxylin, which have been strongly

decolorized, a longitudinal split is evident and likewise a division of the chromosome into chromomeres. If the chromosome is of the second type and seen from above, two of the chromomeres will be seen longitudinally split (Fig. 46; cf. Fig. 53). An end view of a chromosome of the first type shows simply a single chromomere longitudinally split (Fig. 59).

Linin connections between the chromosomes are much more evident than in the spermatogonia, and they can be seen to extend from the sides as well as the ends of the chromosomes.

With regard to the origin of the first maturation spindle-fibres it is difficult to be certain, but they appear to arise, at least in part, from within the nucleus. The centrosome is not evident until a rather late prophase (Figs. 39, 40, 43). In many cases it lies within a more densely staining mass of cytoplasm of ill-defined outline applied close to the nucleus (sphere substance, idiozome of Meves) (1898) (Figs. 39*a*, 43). This is not, however, invariably the case, as may be seen from Figs. 40, 39*b*, where the centrosomes lie freely in the cytoplasm. Fig. 38*b* perhaps represents an early stage in the development of the sphere substance. In the two adjacent cells (Fig. 38*a* and 38*c*) are shown rounded bodies of a dull tint lying within clear vacuoles. I met these in but one preparation and am unable satisfactorily to interpret them. The division of the centrosome and the formation of the spindle is shown in Figs. 46, 47, 48, 52. The centrosomes and spindle-fibres, as well as the polar radiations, are more prominent than in the spermatogonic spindles. During this time the sphere substance disappears.

In the equatorial plate the chromosomes become arranged with the longitudinal split parallel to the axis of the spindle in the case of chromosomes of the first type, but at right angles to it or nearly so in the case of chromosomes of the second type (Figs. 49, 50 and 53). In Figs. 55 and 56 are represented pole views of both types of chromosomes. It may be gathered from these, as well as from the figures of the prophases, that chromosomes of the second type are not nearly so numerous as those of the first nor so numerous as those of the intermediate type.

From what has been said with regard to the origin of the chromosomes, it will be seen that in the metaphase the bivalent chromosomes are separated into their univalent components, and consequently the *first division is one of reduction*.

A well-marked mid-body is visible in the late anaphase (Fig. 61a). The interzonal fibres are sharply constricted and oftentimes the nuclei completely separated before a cell wall makes its appearance. In stages like this a noticeable bending of the fibres is often observed. This is slightly evident in Fig. 61a.

Apparently the plane of the second spermatocytic division is to be at right angles to the first, if Figs. 61a and 61b are interpreted as early stages in the formation of the equatorial plate of the second spermatocyte.

The equatorial plate of the second spermatocytic division is shown in lateral view in Fig. 62. The length of the chromosomes is less than that of the chromosomes of the first spermatocytic division. The question as to whether the second division is actually equational is difficult to decide. The chromosomes of the first maturation figure, consisting of a double row of four granules, are separated by karyokinesis into halves, and each half contains a double row of two granules (Fig. 58). It thus has the appearance, although only the appearance, of a true tetrad. It will be seen that some of these daughter chromosomes have a length equal to their width, whereas in others the length is slightly greater than the width. If we turn to the fully-formed spindle of the second division (Figs. 62, 63) we find similar phenomena. It might be argued from these appearances that the second division is also reducing. In view, however, of the weight of evidence in favor of both methods of division (equation and reduction) being necessary to the maturation of the sexual cells among the Arthropods, I hesitate to accept this interpretation without further corroborative evidence. When the length of the chromosomes is equal to their breadth, it is obviously as impossible to decide here concerning the plane of division as in the case of the true tetrads of the Copepods, *Canthocamptus*, *Heterocope* or *Diaptomus*. If the length is greater, as in the anaphase, the appearance might be referred to the elongation of the mother chromosome (Figs. 49, 51, 53), some of the daughter chromosomes not having recovered from the stretching apart of the chromatin in the metaphase. The apparently greater length of some of the chromosomes in the spindle of the second division (Fig. 63) may be explained by the assumption that some of the chromosomes commence to divide earlier than others, and consequently become elongated, an assumption which is not without parallel in the first spermatocytic and especially in the sperma-

togonic divisions (Fig. 15). In Fig. 61, a stage intermediate between 58 and 62, some of the chromosomes likewise appear of greater length than others. It might be supposed that the longer ones represent the side view, the shorter ones the end view, of the chromosomes. This need not, however, necessarily be the case, for the chromosomes vary amongst themselves in size (Fig. 58 and previous figures). It is possible, too, that in some cases the chromosomes are seen slightly foreshortened and that their true dimensions do not appear in the figure. I feel it, therefore, impossible to ascertain with the desired degree of certainty the plane of the second spermatocytic division.

In the late anaphase (Fig. 66) the chromosomes are more or less indistinguishably massed together. On each of the interzonal fibres in the equator is a minute swelling. These become reduced in number (Fig. 67).<sup>1</sup>

#### 4. *Metamorphosis of the Spermatids.*

The chromosomes spread apart, a nuclear membrane is developed and the daughter cells become the spermatids. The gradual conversion of the chromosomes into a fine reticulum is illustrated in Figs. 69 and 70.

The nucleus now commences to elongate at one end (Fig. 72), and this continues until the entire nucleus is transformed into a shape somewhat like that of a narrow flask (Fig. 74). The nuclear network is extremely delicate and takes the iron hæmatoxylin stain more faintly than previously. In cross section (Fig. 74*b*) numerous fine dots appear interspersed with clear areas (vacuoles). This vacuolated appearance is sometimes evident at an earlier stage (Fig. 71).

During the transformation of the nuclei the cell boundaries have entirely disappeared and the nuclei lie in a common mass of cytoplasm. Several of them become associated together, and their extremities, elongated into slender threads, are surrounded by a clear, homogeneous, well-defined area of cytoplasm, while the more or less contorted bodies of the nuclei still lie in an undefined mass of cytoplasm (Fig. 77*a*).

A cytoplasmic thread of extreme delicacy can be traced from the

<sup>1</sup> During the examination of the foregoing stages I have seen nothing similar to the accessory chromosome (chromatin nucleolus) of insects, as described by Montgomery (1898) and Paulmier (1899).

slender extremity of each nucleus for some distance into the clear, homogeneous area (Fig. 77a). At this stage also there can be clearly seen in the undefined mass of cytoplasm a bundle of fibres, which run in between the nuclei, but which cannot be seen to have any connection with them. I have a preparation of a stage, earlier than that just described, stained with hæmatoxylin and Bordeaux red, in which these striations appear, near the margin of the follicle (Fig. 73). So early a development of the fibres is rather unusual. The fibres are here apparently incomplete and not massed together as they later are. On account of their indistinctness it is difficult to say whether or not they are independent of the nuclei. At first sight it might appear as if they were continuous, but it is impossible to state definitely that this is so because of the impracticability of tracing a single fibre for any great distance.

The further changes in the nuclei consist in their gradual elongation into filaments, in which the network has entirely disappeared and which have acquired the power to take a vivid and homogeneous stain. Their free ends, at first divergent, gradually approach each other and finally come to lie close together (Figs. 77-79, 85 and 86). In regions of the follicle where the cells are closely crowded together the nucleus is often seen to be bent or coiled upon itself (Fig. 83).

There is at first a small quantity of cytoplasm around the nuclei, but as they increase in length this disappears. The cytoplasmic fibres also increase in length at the expense of the surrounding cytoplasm. Their length, indeed, becomes truly marvelous, many times exceeding that of the nuclei. They crowd in between the follicle cells (Fig. 2) and in cross sections of the follicle can be seen in great numbers around the margin. From the anterior end of the bundle is developed a slender flagellum (Figs. 85, 86). The entire bundle has the appearance at first sight of a single spermatozoon, and such I thought it before having studied its development.

The term "spermatophore" has been applied by Gilson to the bundle. This term, however, has been used by Grobben and others to designate an envelope secreted by the cells of the vas deferens (in the Decapods) and surrounding a mass of spermatozoa. It does not, therefore, seem applicable to the bundle of spermatozoa found in the Oniscidæ. Ballowitz applies the term "spermozeugma" to a large bundle of double spermatozoa found in the vas deferens



of the Dytiscid, *Colymbetes striatus*. These adhere together after having reached maturity. Their structure and mode of origin is, therefore, not the same as that of the bundles of Oniscus. The term "compound spermatozoon" has been suggested to me, but the word spermatozoon might carry with it certain implications with regard to behavior in fertilization. I prefer, therefore, to use the term sperm colony, at least until a better one offers itself. Gilson uses this term also, although not so generally as the word "spermatophore."

The number of nuclei entering a colony varies within rather wide limits. I have counted as few as six and also as many as fourteen. In cross sections stained with safranin and malachite green, they are seen as red bodies surrounding a central mass of green dots, the sections of the cytoplasmic fibrils (Fig. 8o). The red dots diminish in size toward the anterior end of the bundle, and at one point can be seen merging directly into delicate green threads (Fig. 8oδ). At the extreme anterior end of the bundle the delicate green threads alone will be cut (Fig. 8oα). It might be supposed that the bundle of cytoplasmic fibres previously described are the tails of the spermatozoa. If they are really the tails of the spermatozoa, one would expect to find them at some place connected with the nuclei, or with the delicate fibres which can be demonstrated to be continuous with the nuclei. A comparison of sections obtained at different levels seems to leave but two alternatives: either the long bundle of cytoplasmic fibres stops abruptly before the anterior end of the colony is reached, or the connection is of so tenuous a character as to escape observation. In structures of such minuteness the latter might easily be the case.

A point bearing on this matter, and therefore of interest to determine, is the number of cytoplasmic fibres as compared with the number of nuclei. Attempts to determine this might be made in two ways. The mature sperm colonies taken from the vas and teased apart might be examined and an attempt made to count the fibres at the frayed end of the bundle, or one might try to count the number as seen in cross sections. By either method it is difficult to be sure of an accurate count, for in the frayed ends of colonies one or more of the fibres may adhere together. In cross sections the fibres appear as minute dots, as a rule, closely crowded together. Occasionally they may be more loosely distributed. Fig. 81δ represents a cell of this sort in which the number of cyto-

plasmic fibres equals that of the nuclei. I cannot be certain that this is invariably the case. With the iron hæmatoxylin stain the bundle of cytoplasmic fibres stains deeply, like the nucleus, and it is therefore impossible to distinguish between them in cross section where both appear. The delicate fibril previously mentioned, which joins the nucleus, stains faintly and can therefore be distinguished from the nucleus. In Figs. 81 and 82 cross sections of sperm colonies at slightly different stages of development, colored with this stain, are compared. In both images may be seen similar to that of Fig. 80—*i. e.*, a circle of dots merging into faintly staining fibres. Sometimes the latter have a granular or beaded structure (Fig. 81*a*). These are sections near the anterior end of the colony, and here again the central circle of dots, representing the posterior cytoplasmic fibres, is lacking. Fig. 82*b* represents a section which I interpret as having been cut slightly posterior to Fig. 82*a*. The tail fibres here begin to appear.

A comparison of the two stages illustrates the gradual dwindling of the cytoplasm which surrounds the bundle. It will be remembered that shortly after the complete reconstruction of the spermatid nucleus, cell boundaries disappear and the nuclei lie in a common plasma. When, however, the nuclei come to be associated in groups, the cytoplasm again becomes sharply defined and in cross sections an appearance like that of separate cells is obtained (Fig. 80). The cytoplasm in the anterior region becomes comparatively homogeneous and the nuclei often lie in a central clear space (Fig. 81*a*). More posteriorly it breaks up and assumes a granular appearance (Fig. 81*c*), while still farther back the fibrillar bundles lie isolated, with vague remnants of cytoplasm between them (Fig. 81). In Fig. 82 the diameter of the colony is less and the cytoplasm surrounding the fibres decidedly less extensive.

The sperm colonies when mature, or nearly so, are forced into the vas deferens, probably by contractions of the muscle layer of the follicle. In the vas they are surrounded by a fluid secreted by the large cells which form its lining, and which causes them readily to adhere to needles or forceps. The mature colony has the appearance shown in Figs. 85, 86 and 87. I have not been able to isolate a single colony entire, for in teasing the long fibres are almost invariably torn. I have been able to trace them for a considerable distance, however, and can state that they are exceedingly long. The filamentous nuclei are invariably partially frayed from the

sheath and often entirely torn from it, lying twisted and contorted at some distance from the sheath. According to Hermann, 1883 (2), the spermatozoa of the Isopods retain their immobility in the oviduct of the female. The function of the extraordinarily long fibres, if the spermatozoa remain motionless, is to me a matter of great perplexity. It becomes still more puzzling if, as my preparations seem to indicate, there is no direct connection between them and the nuclei. Their function and their true relation to the nuclei might possibly be elucidated by a study of their behavior in fertilization, a study in which I hope to engage at some future time.

##### 5. *The Nucleolus.*

In the resting spermatogonia the nucleolus is present as a rounded or oval body, staining pink with the eosin of the Biondi-Ehrlich stain and red with safranin. When the mitotic figure is fully formed it is, as a rule, no longer visible, nor is it seen in the prophase immediately preceding. The newly constructed daughter nuclei likewise show no trace of it (Figs. 10, 14, 20). Possibly it may consist of metabolic products developed in the resting cell and quickly dissolving during or before mitosis. In the synapsis stage, subsequent to the last division of the spermatogonia, the nucleolus is, however, clearly visible, lying to one side of the tangled mass of chromatin threads.

In the very earliest synapsis of which I have sections it is not discernible (Fig. 22), but as the threads elongate and separate it becomes evident. It continues to be present throughout the synapsis and is finally enclosed within the nucleus of the resting spermatocyte by the development of the nuclear membrane (Figs. 23, 26, 28, 29 and 30). Throughout the prophases of the first spermatocyte it is still to be seen within the nucleus (Figs. 32, 33 and 43a), and after dissolution of the nuclear membrane and formation of the mitotic figure it is cast off to one side of the spindle, where it persists for some time (Figs. 47, 51, 52, 55, 61, 65-67 and 69d). With safranin and malachite green the nucleolus is very evident, coloring bright red, while the chromatin of the resting cell is purple. With iron hæmatoxylin it is not so readily distinguished, but with the Biondi-Ehrlich stain it can be seen as a pink body lying to one side of the spindle.

### 6. Summary.

The main results of this study may now be briefly summarized as follows :

(1) The spermatogonic chromosomes are joined together in pairs in the synapsis to form sixteen bivalent chromosomes. They may be joined (*a*) in an approximately straight line, (*b*) to form a more or less narrow V, or (*c*) into a more or less complete ring (Figs. 26, 27).

(2) A longitudinal splitting of the chromatin threads takes place at this stage (Figs. 25*a*, *b*, *c*).

(3) The distinctness maintained by the chromosomes up to the formation of the nuclear network of the resting spermatocyte, and the manner of origin of the spermatocytic chromosomes from it, lends support to the theory of their individuality in the resting nucleus (Figs. 28 and 32).

(4) In the structure and mode of origin of the bivalent spermatocytic chromosomes two main types may be distinguished : (*a*) The component chromosomes lie end to end, or (*b*) they lie side by side (Figs. 68*a*, *b*, *c*).

(5) Inasmuch as univalent chromosomes are separated, the first maturation division is reductional (Figs. 48-59).

(6) Sphere substance (idiozome) is not observable, except for a short time during the prophases of the first spermatocyte (Figs. 39 and 43).

(7) The nucleolus of the spermatogonia disappears shortly after dissolution of the nuclear membrane, while that of the spermatocytes, first discovered in the synapsis, persists throughout the divisions (Figs. 8-10, 47, 26, 29, 33, 47, 48, 51, 52, 55, 58, 60*a*, 61, 65-67, 69).

(8) The spermatids become associated in groups to form colonies of nuclei lying in a common plasma (Figs. 73-75).

(9) Within the latter arise bundles of fibres of great length, whose connection with the nuclei, if actual, is very slight and occurs very late, as well as single fibres of greater delicacy which are continuous with the nuclei (Figs. 76-83).

(10) The mature sperm colony consists of a variable number of filamentous nuclei contained, together with the bundle of cytoplasmic fibres, in a tenuous sheath which is flagellate at its anterior extremity (Figs. 84-86).

### III. CRITICAL REVIEW OF THE LITERATURE ON CRUSTACEAN SPERMATOGENESIS SINCE 1878.

#### I. SPERMATOZOA.

##### a. Review.

##### *Decapoda.*

1878. Grobben in his valuable work investigates principally the form of the Decapod spermatozoa and their transformations from the immature to the mature state, as well as the nature of the case (spermatophore) in which they are enclosed. With regard to the spermatozoon of *Astacus fluviatilis*, he states that the head develops from a structure arising near the nucleus, while the nucleus itself disintegrates. He gives also a review of the literature on Crustacean spermatozoa up to that time, which therefore need not be repeated here.

1883 (1). Herrmann describes the spermatozoa of the Podophthalmia, chiefly the *Macrura* and *Brachyura*. The study of the development, he says, shows a series of transitory forms which enable us to seize clearly the bonds of relationship existing between the different adult forms. The transitional forms of some resemble the complete forms of others.

1884. Nussbaum (*Astacus fluviatilis*) considers the change of the spermatid into the spermatozoon. He traces the gradual condensation and transformation of the nucleus from spermatid to spermatozoon, and the transformation of a large body lying in the cytoplasm into the peculiar "kopfkappe" of the mature spermatozoon (see his Figs. 53-68). He regards the nucleus as the head of the spermatozoon.

1885. Sabatier published a short article on the spermatogenesis of the Decapod Crustacea, principally *Astacus*.

1886. Gilson describes the spermatozoa of a considerable number of Decapod species, among others *Astacus fluviatilis*. The structure of the spermatozoon of the latter he delineates more fully than either of his predecessors. The nucleus he shows to be present and saucer-like in shape. It is covered by a layer of protoplasm which is extended laterally into pseudopodic processes. From the centre of the protoplasmic layer sometimes arises a protuberance, to which he gives the name "globule achromatique." The nucleus surmounts a bladder-like vesicle often perforated at the opposite pole. Into this from the centre of the concavity of the nucleus projects what he calls "la tigelle."

1895. Auerbach compares the spermatozoon of *Astacus fluviatilis* with those of other Crustacea, Insects and Vertebrates, with a view to discovering homologies of head, apex, middle-piece and tail. The cyanophilous, saucer-shaped nucleus corresponds to the head of more highly developed spermatozoa, its pole therefore to the anterior end of a flagellate spermatozoon and the surrounding protoplasm to the sheath of the head. The "globule achromatique" of Gilson is the anlage of the apex. The "tigelle" of Gilson, which Auerbach found to be erythrophilous, he regards as the anlage of the middle-piece. In the genera *Pagurus*, *Eupagurus*, *Clibanarius* and *Ethusa* the "tigelle" is prolonged into what Auerbach regards as a rudimentary tail. The bladder-like vesicle is perhaps a kind of "Schwanzkappe," possibly comparable with the sheath sometimes surrounding the place of origin of the tail in immature vertebrate spermatozoa. The extremity regarded by Grobben as the head would, according to Auerbach's interpretation, be the tail end. For a more detailed account of the Decapod spermatozoa, of which that of *Astacus* may be taken as a type, the reader is referred to the works cited above.

*Stomatopoda, Schisopoda, Amphipoda.*

1885. Gilson, in his excellent and very comprehensive work, describes also the spermatozoa of the Stomatopod *Squilla*, the Schisopod *Mysis* and the Amphipod *Gammarus*. The whip-like spermatozoon of *Mysis* is strikingly similar in shape to that of the Isopods. That of *Gammarus* is flagellate and that of *Squilla* vesicular.

*Isopoda.*

1883. Herrmann studied among the Isopoda, *Ligea*, *Idotea* and *Sphæroma*. His description is unaccompanied by figures and is difficult to comprehend. The spermatid filaments, he says, are united in numbers varying from eighty to one hundred. The bundles are found lying amongst the cells which line the walls of the tube. He did not find isolated spermatozoa, except in the oviduct of the female, where they retain their habitual form and immobility. The large cell of the vas deferens he considers as homologues of ovarian cells and calls them "ovules males."

1884-1886. Gilson (*Oniscus asellus*). Groups of six spermatids

("spermatoblaste") were observed surrounding a protoplasmic stem and their origin referred to the small cells in the apical portion of the cæcum. The structure of the nuclei and the changes in them and in the surrounding protoplasm, by which the mass is converted into the mature "spermatophore," are described at some length and illustrated with numerous figures. The name "spermatophore" is applied for the following reasons: "Les cellules spermatozoides sont donc contenus dans un étui resistant derivant de la differentiation du protoplasm, c'est-a-dire dans une production particuliere, on pourrait donc appliquer aux faisceaux la denomination de spermatophore." The name "plasmodium pariétal" is applied to the follicle cells and the surrounding protoplasm, and to it is ascribed the function of taking part in the formation of the tails, thus reinforcing the insufficiency of the protoplasm of the germ cells. The tails of the spermatozoa are thus thought to arise in the plasma and to attach themselves to the nuclei "vers le haut." The exact level is not determined. The form of the spermatozoa is compared to that of a whip, the long tail representing the handle and the nucleus the lash. This would seem to indicate that the tail is conceived as being attached to the nucleus at its upper extremity. The entire bundle is said to measure  $0.15\frac{1}{8}$  mm.

The sheath (étui) enclosing the spermatozoa is most evident at the anterior end. The apparent absence of protoplasm around the filamentous nuclei is explained as perhaps due not to degeneration or absorption of the protoplasm, but to a condensation and fusion with the nucleus, perhaps applying itself so closely to the filament that an effect of refraction communicates to it the same coloration. This hypothesis is based on results obtained by treating the flagellæ with nuclear solvents. When submitted to the action of potassium carbonate in concentrated solution or strong hydrochloric acid for several days the filaments become scalariform; a skeleton formed of little chambers is seen which communicate with each other, and which were previously filled with the nuclear substance. The characteristic frayed appearance of the bundles is thought to be due to artificial rupture.

The nuclear flagellæ are said to grow considerably after having attained their distinctive form. From the figures given to show this (Figs. 329 and 330, Pl. VIII), it seems probable that this appearance may be due to a portion of the filaments having been broken off by teasing.

The large cells lining the vas deferens are described and also the smaller cells between them. The latter are believed to arise from the larger ones by segmentation. The function of the large cells is said to be the secretion of the fluid which bathes the spermatozoa. The nucleus of these cells is figured as a network of great regularity.

The mature colony of Asellus, as figured by Gilson in Vol. 2 of *La Cellule*, Pl. X, Figs. 385-395, agrees with that of Oniscus in general appearance. The spermatozoa in the bundle, however, are more numerous and much less compactly bound together. Associated with them in their development is a large cell ("noyau femelle"). The tail is shown to be distinctly continuous with the nucleus. The granular mass surrounding the nucleus at its free end is said to consist of caryoplasm and the remains of the nuclear membrane. Its formation is shown in Figs. 387-393.

A few figures are also given of Idotea.

1886. Wielowieyski, in a short paragraph concerning Asellus, states his opinion that the "noyau femelle" of Gilson is an artificial product, caused by the confluence of the protoplasmic mass with one of the large cells on the margin of the testicle.

#### *Cirrepedia.*

1886. Gilson figures the spermatozoa of *Lepas anatifera* and *Balanas perforatus*. They are flagellate, the nucleus a slender thread occupying the anterior end.

1894. Ballowitz, K., studied *Balanas improvisus* Darw. and *Lepas anatifera* L. He makes the astonishing statement that the head is demonstrable as a distinct structure neither by its form nor by its staining reaction. He mentions the work of Nussbaum (1890) on a Californian Cirrepede (*Pollicipes polymerus*) in which the head is described.

#### *Copepoda.*

1895. Steuer gives a figure to show the spermatozoa of the marine Copepod, *Sapphirina gemma*. They are flagellate, shaped somewhat like a javelin. He mentions the spermatozoa of the *Calanidæ* as being of spherical shape.

#### *Ostracoda.*

1886. Stuhlmann. The spermatozoa of the *Cypridæ* are described as having at first the shape of a ribbon, through the length



of which the nucleus runs as a thread. They are stated to increase in size through the assimilation of a secretion of the vas deferens. They then become spirally twisted while in a certain limited section of the vas deferens, presumably by a motion of their own. This is said to be caused by a fibre running spirally the length of the spermatozoon. The mature spermatozoon has the spirally twisted structure of a rope of tow. It contains a twisted central fibre, not visible externally, and the entire structure is surrounded by a hyaline sheath. The spermatozoa are nearly motionless while in the body of the male, but become extremely active in the receptaculum seminis of the female. This is said to be due to the loss of the hyaline sheath. The curious fact is noted that the spermatozoa coming from the right side of the animal are twisted to the left and vice versa.

1889. Müller discovered in the spermatid of Ostracoda one or two "Nebenkerne." These form a "Schwanzstück" which grows very long and is of complicated structure. Through the middle of the tail runs the central fibre, at or near one end of which the nucleus is located. The spiral twisting is referred to the contraction of the middle one of the three threads which surround the central fibre. He does not agree with the opinion of Stuhlmann concerning the inhibitive function of the sheath while in the body of the male.

#### *Phyllopoda.*

1885. Zacharias describes the results of his observations and experiments on the spermatozoa of the Phyllopod, Polyphemus, which he shows to be capable of amoeboid movements.

#### *b. Commentary.*

The Crustacea as a class show an astonishing variety in the form of the male reproductive elements. Knowledge of their intimate structure is of course at present too incomplete to enable us to discuss at any great length the homologies existing between them. But a rough classification of them according to their external appearance would place the bell-shaped or vesicular form characteristic of the Decapods in one group and the form found in the Isopods, Gammarus, Mysis and Balanus, with more or less elongated nucleus and tail of varying length, in another. The extremely peculiar form of the spermatozoon of the Ostracoda might perhaps be referred to the

latter group. It is possible, and I advance it simply as a tentative hypothesis needing corroboration, that these strikingly dissimilar forms have arisen from a primitive one, simple and amoeboid in character like that of *Polyphemus*.

The ingenious series of homologies drawn by Auerbach between the head, tail, apex and middle-piece of the spermatozoa of Vertebrates and Insects and similar structures in *Astacus* appears plausible. Since, however, the location of the centrosome and the sphere substance remains undetermined, the homologies cannot be said to be in all respects established. A more detailed and thorough examination of the spermatozoa of the Crustacea, especially of their behavior in fertilization, might extend these homologies. If the spermatozoon of *Oniscus* be compared with the type most frequently occurring in animals, the part immediately adjacent to the nucleus, the delicate fibril shown in Figs. 77*a*, 79, corresponds in location to the middle-piece. Whether this is in reality the habitation of the centrosome might be discovered through a study of its fate during fertilization. My observations on the spermatogenesis throw no light on the question.

The Isopods are unique among the Crustacea in the formation of colonies of spermatozoa of a nature so close that they appear as units. Concerning their origin in *Oniscus*, I can confirm M. Gilson's statement that the formation of the bundle takes place in a plasmodium, cell boundaries being for a time entirely absent, and with the main outlines of his account of the changes taking place in the development of the spermatids into the mature colony I am thoroughly in accord.

The number of nuclei entering into a bundle, according to my observations, is not invariably six, but may vary within considerable limits. The number of cytoplasmic fibres is assumed by M. Gilson to be equal to the nuclei, but in his Fig. 328, Pl. VIII, they are shown to be more numerous. As has been already said, I have been unable to convince myself of a direct continuity between these fibres and the nuclei. In his Fig. 320 (an immature spermatophore) the cytoplasmic fibres may be traced directly to the nuclei. I have, however, not been able to obtain images of equal clearness from my preparations. Nor have I obtained anything at all similar to the rings or vacuoles, shown in Gilson's Figs. 328, 329 and 330, near the anterior end of the bundle. In *Sphæroma serratum*, Gilson states, the continuance of head and tail is very evident, forming an

open and regular ring. The close relationship of nucleus and cytoplasmic fibre in *Oniscus* is shown only in Fig. 320. In Figs. 323 and 326 they are represented as discontinuous. In Fig. 334 (*Asellus*) the fibres are pictured as arising independently of the nuclei, although it is shown in later figures that they eventually become attached. If the follicle nuclei and the surrounding protoplasm take part in the formation of the tails, it is only, in my opinion, in so far as they become converted into the substance of the germ cells.

In attempting to reconcile the fact of the direct continuity of head and tail, shown by Gilson so clearly in *Asellus* and stated by him to be present in *Sphæroma*, with the lack of demonstrable connection in *Oniscus*, it occurred to me that the condition in *Oniscus* might represent a different phase in the evolution of the Isopod spermatozoon. Either the connection, at one time evident, between the nucleus and the unusually long tail may have grown so slight as to be no longer recognizable, or, if the spermatozoon of *Oniscus* for any reason is to be looked upon as the more primitive form, it may be that the connection, which will later in the course of evolution become more marked, is as yet but little developed. Although in the present state of our knowledge both alternatives may perhaps be considered open, the former seems to me far more plausible, for not only are the land Isopods in other structural peculiarities to be regarded as more specialized than *Asellus*, but the sperm colony itself in *Asellus* is less compact and less completely developed as a unit. The obscurity of this point serves to emphasize the desirability of further study of the Crustacean spermatozoa and the establishment of accurate homologies between them.

The "noyau femelle" of *Asellus* is, in my opinion, to be regarded as homologous with the follicle cells of *Oniscus*. I am inclined to doubt the correctness of M. Gilson's conclusions as to the origin of the small cells of the vas deferens of *Oniscus* from the larger ones by segmentation, and, although I have not devoted much time to the elucidation of the point, I think it more probable that the reverse is true, for I have seen the small cells segmenting, but never the large ones.

## 2. THE EARLIER STAGES IN THE DEVELOPMENT OF THE GERM CELLS IN CRUSTACEA, WITH ESPECIAL REFERENCE TO THE PROBLEM OF REDUCTION.

### *a. Review.*

#### *Decapoda.*

1878. Grobben gives almost no figures of the earlier stages and does not consider the subject in detail.

1884. Nussbaum (*Astacus fluviatilis*) does not distinguish between spermatogonia and spermatocytes. Five figures of mitoses are given in which the chromosomes are shown to be spherical at the beginning of the metaphase, but they soon elongate to a rod-like shape.

1885. Carnoy studied among the Decapods, *Astacus fluviatilis*, *Crangon vulgaris* and several species of *Brachyura* and *Anomura*. In no case are more than thirteen figures given. It is impossible to determine in every case the generation to which the cells belong. The mode of origin of the chromosomes is not fully traced, and it is impossible to determine with accuracy, therefore, anything with regard to the question of reduction. In the case of *Astacus*, as far as can be judged from the figures given (Figs. 246*a*, *b*, *c*, *d*, *e* and *f*), the division is transverse. The mitosis figured occurred in August, and, according to vom Rath, it is from this month until December that the final divisions of the spermatogonia and those of the spermatocytes take place. A transverse spermatogonic division is improbable. The chromosomes are shown to arise, however, through the shortening and thickening of rods, resulting from the breaking up of the nuclear network. The transverse division, if it be such, is therefore probably that of the first spermatocyte. The same is perhaps true of *Crangon cataphractus* (Figs. 247 and 248). Of peculiar interest is the constitution of the chromosomes of *Crangon cataphractus*, as shown in Figs. 249*a*, *b*, *c*, *d*, Pl. VII. According to these a chromosome in longitudinal view consists of a double row of from three to five granules. A reconstruction of the chromosome from these figures leads to the conception of a rod split longitudinally several times.

**Cytoplasmic Structures.**—A dense mass, lying within the cytoplasm during the prophase and migrating to the poles of the spindle as it is formed, is shown for *Crangon*. No centrosome is figured as lying within this mass, to which the name "Nebenkern" is given. The same name is applied to a body lying in the cyto-

plasm in *Astacus*. This body, however, seems not to be affected by mitosis, but lies passively to one side. In the vicinity of the poles are, however, numerous granules ("corpuscles polaires") (Fig. 246f, Pl. VII). The "Nebenkern" of Crangon, according to the description, behaves like the substance designated idiozome by Meves. The "corpuscles polaires" of *Astacus* may be of a similar nature. For the other forms studied no bodies of any kind lying in the cytoplasm are shown. The substance seems to be unusually prominent in Crangon and *Astacus*. The cells of both are of large size.

1891. vom Rath settled the question of amitotic division of the germ cells of *Astacus* in the negative. He states that a minority of the spermatogonia undergo no change at first, but give rise by mitosis to new spermatogonia after the discharge of the ripe spermatozoa. He mentions a case of regeneration of an entire follicle from a single spermatogonium. With the first appearance of the spermatids the follicle cells ("Randkerne") commence to grow in size and divide amitotically. The direct division apparently takes place by a sharp breaking apart of the portions of the nuclei, resembling a slicing. Degeneration of the nuclei follows. At the point of transition between follicle and duct there is often an extraordinary growth of cells by amitosis. The results of his research are interpreted by vom Rath to mean that two kinds of cells have arisen from indifferent epithelium, one dividing mitotically, the other amitotically.

#### *Isopoda.*

1884. Gilson states that it is only at certain seasons of the year that the spermatogenesis of these animals can be studied with profit. In the case of *Oniscus asellus*, from July to November is the most favorable season for obtaining preparation of what he calls the first stage ("premiere etape"). In the case of *Asellus aquaticus* it is later—about the month of February.

*Oniscus asellus*.—The cells filling the apical end of the cæca (spermatogonia) are mentioned, and the opinion is expressed that they constitute a reserve mass destined to replace by proliferation the elements organized in the lower part of the tube and later evacuated. Karyokinesis in these cells (spermatogonia) was observed but once, and the stages intervening between them and the spermatocytes were not discovered.

The condition of the lower part of the tube is thus described: "Il y aurait dans les cæcums testiculaires des *Oniscus* une sort de plasmodium contenant une grande nombre de noyaux et entourant une masse centrale formée d'éléments spermatiques en formation. Ce fait est si étrange qu'on n'ose à peine l'accepter." The amitotic division of nuclei occupying the lower portion of the follicles and referred by Gilson to the germ cells is probably that of follicle cells, for they are described as occupying the periphery of the tube in its median portion.

1885. Carnoy makes the following statement concerning the Isopods (pp. 222, 223): "Chez l'*Oniscus asellus*, au moment de la plus grande activité cellulaire preludant à la formation des spermatozoïdes, on ne rencontre pour ainsi dire que des noyaux en voie d'étranglement ou de division acinétique. Les figures caryocinétiques y font le plus souvent défaut. Depuis trois ans nous n'en avons rencontré que deux, une couronne équatoriale et une couronne polaire qui sont reproduite dans la Pl. VI, Fig. 227; et cependant nos observations ont été nombreuses et pratiquées à toutes les époques de l'année.

"Nous avons constaté les mêmes phénomènes sur plusieurs animaux du même groupe, sur les *Idotea* en particulier. La division directe est très fréquente chez ces derniers, et s'y fait normalement. Nous n'y avons point remarque de caryocinèse; mais nous devons ajouter que nos observations sur ces Crustacés bien que fait sérieusement ont été beaucoup moins nombreuses que sur *Oniscus*. Chose remarquable, chez les *Idotea* la multinuclearité des grandes cellules qui vont se transformer en autant de faisceaux de spermatozoïdes est due exclusivement à la segmentation du noyau primitive. Ces faits sont d'autant plus singuliers que dans un genre voisin, le genre *Armadillo*, les figures caryocinétiques sont fréquents; tandis que les cas de division directe y sont beaucoup plus rares." I have examined testes of *Armadillo* and also of *Porcellio* and find that they do not differ greatly from *Oniscus* as to the manner and frequency of the divisions.

#### *Copepoda.*

1890, 1892. The work of Häcker on the eggs of *Cyclops* has been corrected by the later research of Rückert and need not, therefore, be mentioned here.

1892. Ishikawa gives a figure of the testis of a *Copepod* cut

longitudinally, showing it to be divided into regions called by him formative, growing and ripening zones. The formative region corresponds in *Oniscus* to the reserve groups of spermatogonia, the growing region to the apical part of the follicle and the ripening zone to the basal part of the follicle. Ishikawa's conclusions concerning reduction have not been substantiated by recent research.

1894. Rückert. This well-known paper concerns the ovogenesis of the Copepods, *Cyclops strenuus*, *Hetercope* and *Diaptomus*.

In *Cyclops* the number of chromosomes is 22-24. The germinal vesicle shows double threads of chromatin, a longitudinal split having occurred at an early period. At the beginning of maturation these contract to double rods, whose number is the reduced one and which have, moreover, become transversely split. As the spindle is formed the chromosomes come to lie in the equator, with the longitudinal split at right angles to the axis of the spindle. The first division is thus equational. In the second division the chromosomes are separated along the transverse split, and this division is therefore reducing.

In *Hetercope* and *Diaptomus* open rings are formed which, through condensation, become the tetrads. The plane of the first division is not so easily determined for these Copepods. In the opinion of Rückert the first maturation division of *Diaptomus* is equational.

1895. Häcker studied the ovogenesis of the Copepod, *Canthocamptus*. The reduced number of chromosomes is twelve. There are apparently two divisions of the ovogonia. The last division is followed (1) by a transverse breaking apart of a doubly split thread and a shortening and thickening of the segments so that twelve double rods are produced. Some of these are transversely split. Or (2) the last division of the ovogonia is followed by a condensation and longitudinal division of the thread as a whole and a subsequent breaking apart of the thread into twelve double rods. These become transversely split and form chromosomes corresponding to the tetrads of the first mode. In either mode the changes follow immediately upon the last division of the ovogonium, and no true reticulum is formed in the germinal vesicle. Since the width of the chromosomes is equal to their length, it is impossible to settle the question as to the order in which the longitudinal and transverse divisions occur.

1895. vom Rath describes the ovogenesis of marine Copepods

mentioned by him in his earlier works on *Gryllotalpa* and *Salamandra*. He studied the genera *Euchæta*, *Eucalanus*, *Anomalocera* and *Pleuromma*. He calls attention to the differences that may exist between the ovogenesis of different species of marine Copepods and between the ovogenesis and the spermatogenesis of the same species. His conclusions on the subject of reduction agree substantially with those of Rückert. Particularly in the case of *Euchæta marina* and *Eucalanus attenuatus* is the aspect of the first maturation figure similar to that of Cyclops. Here, too, the division seems to be equational.

#### *Ostracoda.*

1898. Woltereck describes a well-marked synopsis zone in the ovary of a parthenogenetic Cyprid. He rejects, as not applying to the object which he studied, the theories of Moore, Brauer and Häcker concerning the relation of the synopsis to the last ovogonic division and to the processes of reduction and maturation. "Von 'Reduktion,'" he says, "ist nicht die geringste Andeutung vorhanden, von der Reifungstheilung sind die Eier noch durch eine lange Phase getrennt, in der das Chromatin kaum sichtbar ist und gegen die Auffassung als Dispirem die excentrisch Zusammenballe bei deutlich vorhandenem Nucleolus, sowie das Vorhandensein aller Uebergänge aus einem lockeren, hellen Fadenknauel in die Synopsis und aus ihr in die segmentirten Chromosome."

#### *Phyllopoda.*

1892. Brauer thus summarizes his results on the ovogenesis of Branchipus: "Die Beobachtungen, welche ich bei Branchipus gewonnen habe, zeigen nun folgendes Bild:

"1. Keimbläschen: durch Quertheilung entstehen 6 Schleifen; eine neue Quertheilung erhöht ihre Zahl auf 12. Dann folgt eine doppelte Langspaltung. Resultat: 12 viertheilige Chromosomen bilden die Äquatorialplatte der ersten Richtungsspindle" (p. 53). In describing the Figs. 8 and 9, Taf. I, upon which he bases this conclusion, he says: "Ich will gern zugeben, dass diese Beobachtung schwierig sind und eine Täuschung möglich ist, doch muss ich vorheben, dass ich kein Bild gesehen haben, welches eine Vermehrung der 12 Faden durch eine Quertheilung auf 24 zweitheilige auch nur andeutete und spätere Verklebung von je zweitheilige zeigte. Solche Bilder, welche ganz ähnlich aussehen



müssten wie das in Fig. 1 dargestellte, waren mir, glaube ich, nicht entgangen."

1893. Brauer. The study of the closely related *Phyllopod Artemia* was undertaken by the same author with the object of ascertaining whether reduction took place in parthenogenetically developing eggs.

The number of chromosomes in the germinal vesicle is eighty-four, and their structure is quadripartite, *i. e.*, each consists of four spheres. In the first maturation division two of these spheres are separated from the others. After this has taken place the maturation may proceed in two different ways. The second polar body may be formed and the elements of the dyad separated, or there may be an abortive attempt to form the second polar body, the chromatin, however, remaining undivided and the elements of the dyad not separated.

Cleavage and further development of the egg may take place in both of the above cases. In the first case it is necessary for this that the second polar body be drawn back into the egg, where it acts as would a male pronucleus. In the second case the nucleus left within the egg after the formation of the first polar body, becomes the cleavage nucleus. In the first case the somatic number of chromosomes is 168, in the second case 84.

It thus appears that the tetrads of the germinal vesicle are bivalent chromosomes and that the actual reduction may or may not take place.

1893. Moore published the results of his studies on the reproductive elements in *Apus* and *Branchipus*. With regard to *Branchipus*, the chief stress of the paper is laid upon the relation between karyokinesis and protoplasmic structure, the author believing "that the divisional phenomena of these cells are intimately related to a protoplasmic structure, which might be fitly described as 'Schaum-plasma,' and one of the initial physical impulses toward metamorphosis is a fusion of some of the intra-nuclear globules; and a considerable portion of the complicated karyokinetic figures, with their centrosomes, pseudosomes and dictyosomes, appear to be the logical as well as the actual consequence of the continuance of this process."

The question of reduction is not entered upon in much detail. From the nucleus of the resting spermatocyte, however, are shown to arise ten chromosomes of dumbbell-shape. These become

arranged in the equatorial plate with the transverse constriction in the plane of the equator. This division consequently is apparently reducing. No longitudinal split is shown and the second spermatocytic division is very inadequately worked out.

*b. Commentary.*

Although agreeing with many points in the description of Gilson concerning the metamorphosis of the spermatids of *Oniscus*, my observations do not entirely coincide with his account of the earlier stages. The statement defining the most favorable season for obtaining preparations of the first stage does not hold true for the locality of Philadelphia, for I have sectioned material collected during every month of the year, except December and January, and have not found one month to be preferred over another with regard to the abundance of any particular stage.

I feel sure that the function of replacing the evacuated elements which he ascribes to the spermatogonia is the true one, but that their multiplication takes place by direct division I am unable to believe. On the one hand the weight of the evidence of modern research is against the occurrence normally of amitotic division in the germ cells. Moreover the work of vom Rath on *Astacus* creates a strong probability that the phenomena are similar in *Oniscus*. I have never seen amitotic division in the germ cells of *Oniscus*, and believe that the error arose from a failure to distinguish between the germ cells and the follicle cells. I cannot help a feeling of surprise that mitosis should have been so infrequently seen both by M. Gilson and his colleague, M. Carnoy. It is true that the mitoses of the spermatogonia are scattered, and occasionally no spindles at all will be met with in a follicle, but by cutting a sufficient number of sections cell division will be abundantly seen.

With regard to the question of reduction in the Crustacea, my results, much to my own surprise, do not coincide with those obtained by Rückert and vom Rath in the Copepods. The case in *Cyclops* is so clear that it seems to admit of no doubt, and its very clearness makes it probable that the divisions take place in a similar manner in a form so closely allied as *Canthocamptus*. The figures given by Häcker of this object do not, however, conclusively prove this to be the case, since the tetrads are cubical in shape, the length no greater

than the width. Indeed Häcker himself says of this object that it is not adapted to the solution of the problem of reduction. The like may be said of *Artemia*.

With Brauer's results on *Branchipus*, those obtained with *Oniscus* likewise do not agree. The double longitudinal split claimed by Brauer for the chromosomes of *Branchipus* is not shown in the figures with the clearness that might be desired. An oblique view of an elongated chromosome in Fig. 8 shows it to be split longitudinally, not twice but only once. In the absence of direct evidence to the contrary, the Figs. 8 and 9 might be explained equally well on the assumption that the twelve tetrads represent two univalent chromosomes longitudinally split and joined end to end.

In *Oniscus*, inasmuch as the first division separates two originally distinct chromosomes and the second presumably divides the chromatin longitudinally, the manner of reduction resembles that of *Insecta* as described by Henking (1890-'92), Paulmier (1899) and Montgomery (1898, '99).

If my interpretation of the method of reduction in *Oniscus* be correct, and that of Rückert concerning reduction in *Cyclops* be equally so, it becomes clear that the cell generation in which the true reduction takes place need not be the same for all members of a given class of animals. The order in which the reduction and equational divisions take place is, therefore, relatively unimportant; the significant thing, so far as our knowledge at the present day goes, appears to be that in the *Arthropods* both divisions should take place. Further research alone can show whether the apparent cases of transverse division in the first spermatocytes of *Astacus*, *Crangon* and *Branchipus* are really such. To the future must also be left the question as to which method of reduction, the Copepod or the Isopod type, is the rule among *Crustacea*.

M. LOUISE NICHOLS.

January 10, 1901.

## EXPLANATION OF THE PLATES.

All of the figures, with the exception of 1, 2 and 68, are camera drawings made at the level of the microscope stage, and all except 3, 4a, 5, 6, 84-86, were drawn with a Zeiss homogeneous immersion objective  $\frac{1}{4}$ , ocular No. 6, tube length 100 mm. In those marked \* the chromosomes are not all shown.

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| PLATE XI   | <ul style="list-style-type: none"> <li>1. Free-hand drawing to illustrate the male reproductive organs of one side. <i>a, b, c</i>, lobes of the testis; <i>v</i>, vas deferens; <i>p</i>, penis; <i>x</i>, suspending tissue.</li> <li>2. Lobes of the testis in longitudinal section (semi-diagrammatic). <i>a, b, c</i>, as before; <i>spg.</i>, spermatogonia; <i>f. c.</i>, follicle cell.</li> </ul>  |
| PLATE XII  | <ul style="list-style-type: none"> <li>3. Longitudinal section of the vas deferens (Zeiss ocular 4, obj. AA). <i>b, c</i>, lobes of the testis.</li> <li>4a. Small portion of the wall of the anterior region of the vas (oc. 6 obj. D).</li> <li>4b. Secretory cell from the anterior region of the vas.</li> </ul>  |
| PLATE XIII | <ul style="list-style-type: none"> <li>5. Small portion of a testis lobe in longitudinal section. <i>f. c.</i>, follicle cells; <i>m. l.</i>, muscular layer (oc. 6, obj. D).</li> <li>6. Cells from the suspending tissue (<i>cf.</i> Fig. 1, x) (oc. 6, obj. D).</li> <li>7. (a) Spermatogonium in an early spireme stage; <i>ncf</i>, nucleolus. Centrosomes beginning to divide. (b) Resting spermatogonium with large masses of chromatin, probably beginning to degenerate.</li> <li>*8, *9, 10. Later spireme stages.</li> <li>11. (a and c) Resting spermatogonia. (b) Spireme beginning to segment.</li> <li>12. Equatorial plate in side view.</li> <li>13. (a) Equatorial plate in pole view. (*b) Spermatocytic prophase. <i>m. l.</i>, muscle layer.</li> <li>14. Equatorial plate in side view, showing the longitudinal split in the chromosomes.</li> <li>*15. Metaphase.</li> <li>16. Approximate pole view of a stage similar to 15.</li> <li>17. Anaphase.</li> <li>18. Late anaphase. Mid-body.</li> <li>*19, *20. Reconstruction of the daughter nuclei. In 20 the mid body has migrated to the periphery.</li> <li>*21. (a and b) Reconstruction of the daughter nuclei. (c) Degrating spermatogonium.</li> </ul> |
| PLATE XIV  | <ul style="list-style-type: none"> <li>22, 23-28. Synapsis. 26. 1-16, chromosomes.</li> <li>27. Different forms of the chromosomes in the synapsis.</li> <li>29. Formation of the nuclear membrane.</li> <li>30. Resting spermatocyte. <i>spg.</i>, spermatogonium.</li> <li>31. Irregular arrangement of the nuclear network, occasionally seen just before the formation of the nuclear membrane.</li> </ul>  |

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| PLATE<br>XV | <p>32, *33-47. Prophases of the first spermatocyte. 44. 1-16, chromosomes.</p> <p>46 and 47. Strongly decolorized sections showing the longitudinal split of the chromosomes. Divergence of the centrosomes.</p> <p>48. (a) Side view of the equatorial plate of the first spermatocyte. (b) Anaphase of the first spermatocyte.</p> <p>49-53. Equatorial plate of the first spermatocyte in side view.</p> <p>54. Chromosomes of the first spermatocyte, showing the longitudinal split.</p> <p>55, 56. Pole views of the equatorial plate of the first spermatocyte.</p> <p>57. Slightly oblique view of the same.</p> |  |   |
|             | <p>58. Anaphase (side view).</p> <p>59. Anaphase (pole view).</p> <p>60. Anaphase (tangential sections).</p> <p>61. Telophases.</p> <p>62. Side view of the equatorial plate of the second spermatocyte.</p> <p>63. The same more strongly decolorized.</p> <p>64. Pole view of the same.</p> <p>65. Metaphase.</p> <p>66, 67. Telophases.</p>   |  |   |
|             | PLATE<br>XVI   | <p>68. (a and b) Mode of formation of the two main types of chromosome in the first spermatocyte. (c) Intermediate form.</p> <p>69, 70. Reconstruction of the nucleus of the spermatid.</p> <p>70. Disappearance of the cell boundaries. <math>\alpha</math>, remains of degenerated cells.</p> <p>71. Variation in the appearance of the spermatid nucleus.</p> <p>72. Commencing elongation of the spermatid nucleus.</p> <p>73. Group of spermatids from near the margin of the testis lobe. Appearance of cytoplasmic striations (hæmatoxylin and Bordeaux red).</p> |   |
|             |  | <p>74-79. Further development of the spermatids.</p> <p>74. Stage succeeding 72. (a) Longitudinal; (b) transverse section (iron hæmatoxylin).</p> <p>75. Longitudinal section (iron hæmatoxylin).</p> <p>76. Longitudinal section (Biondi-Ehrlich). The middle figure alone is complete anteriorly.</p>  |   |
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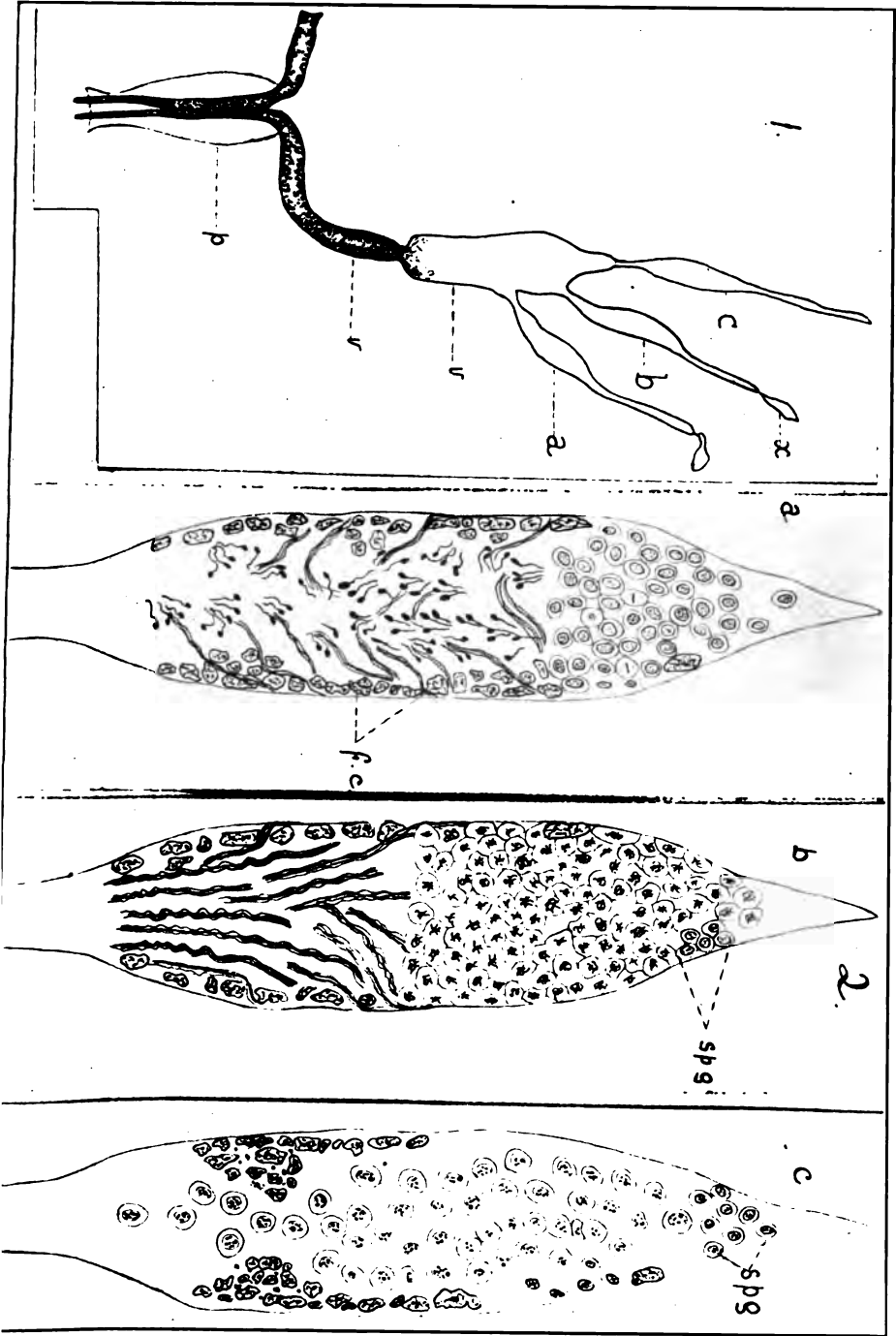
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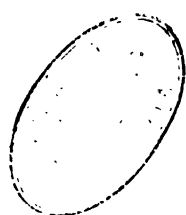
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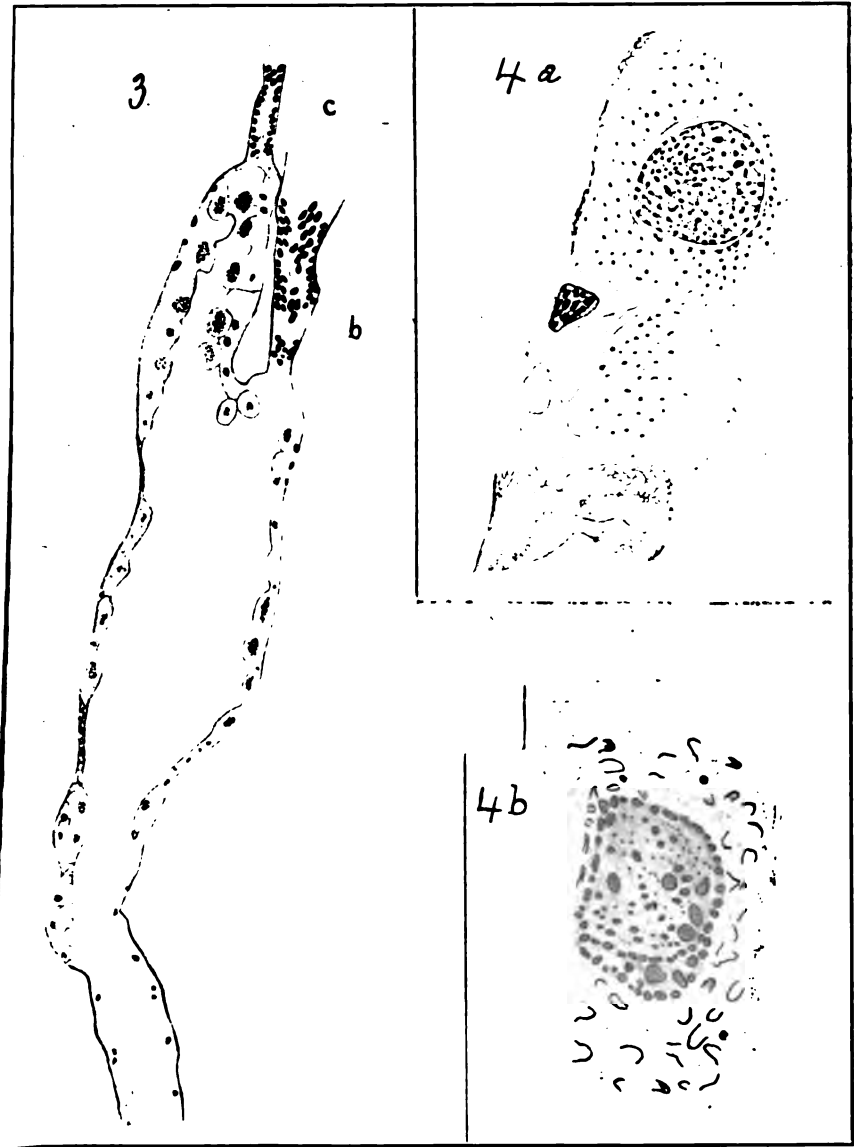
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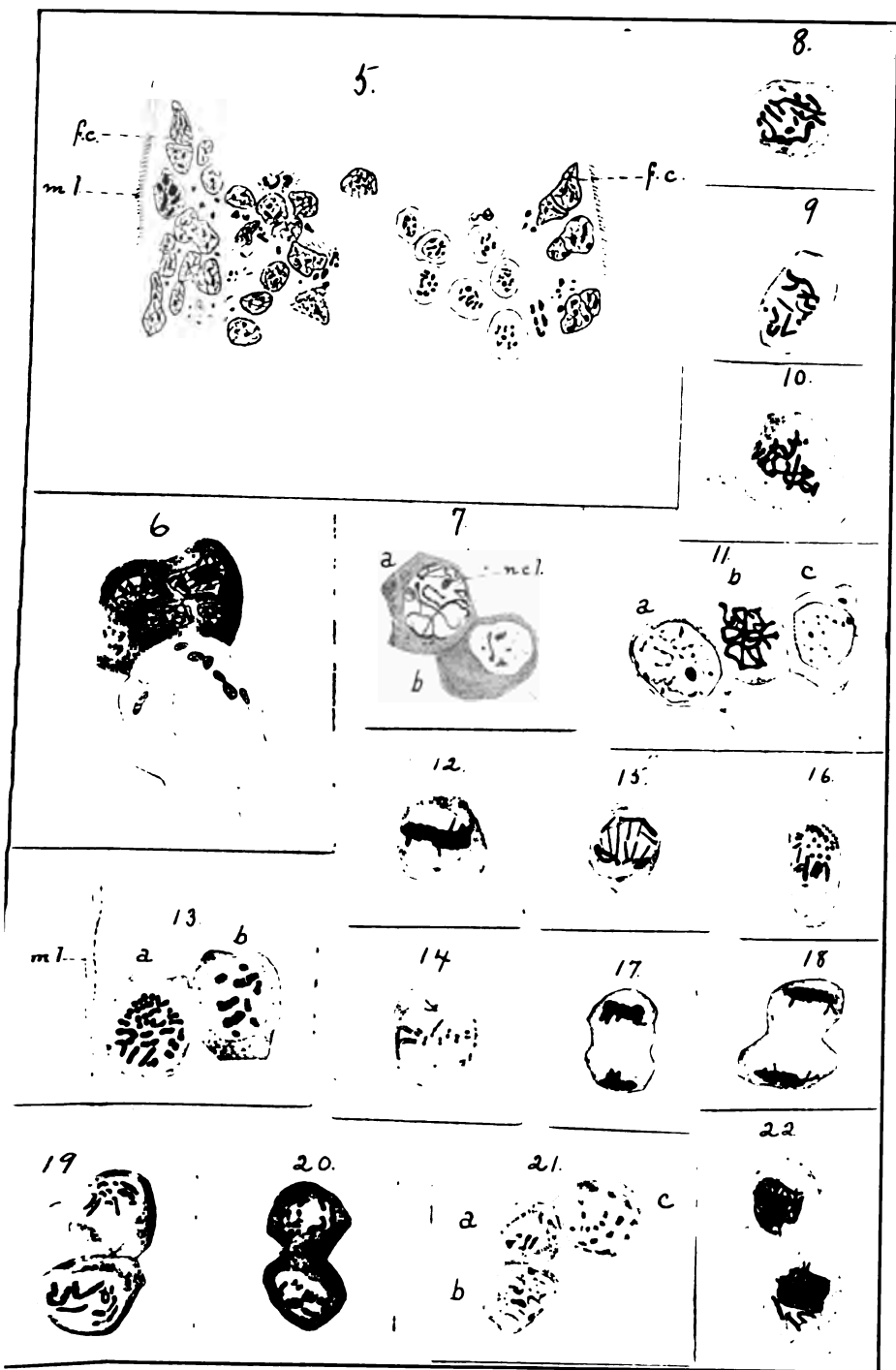
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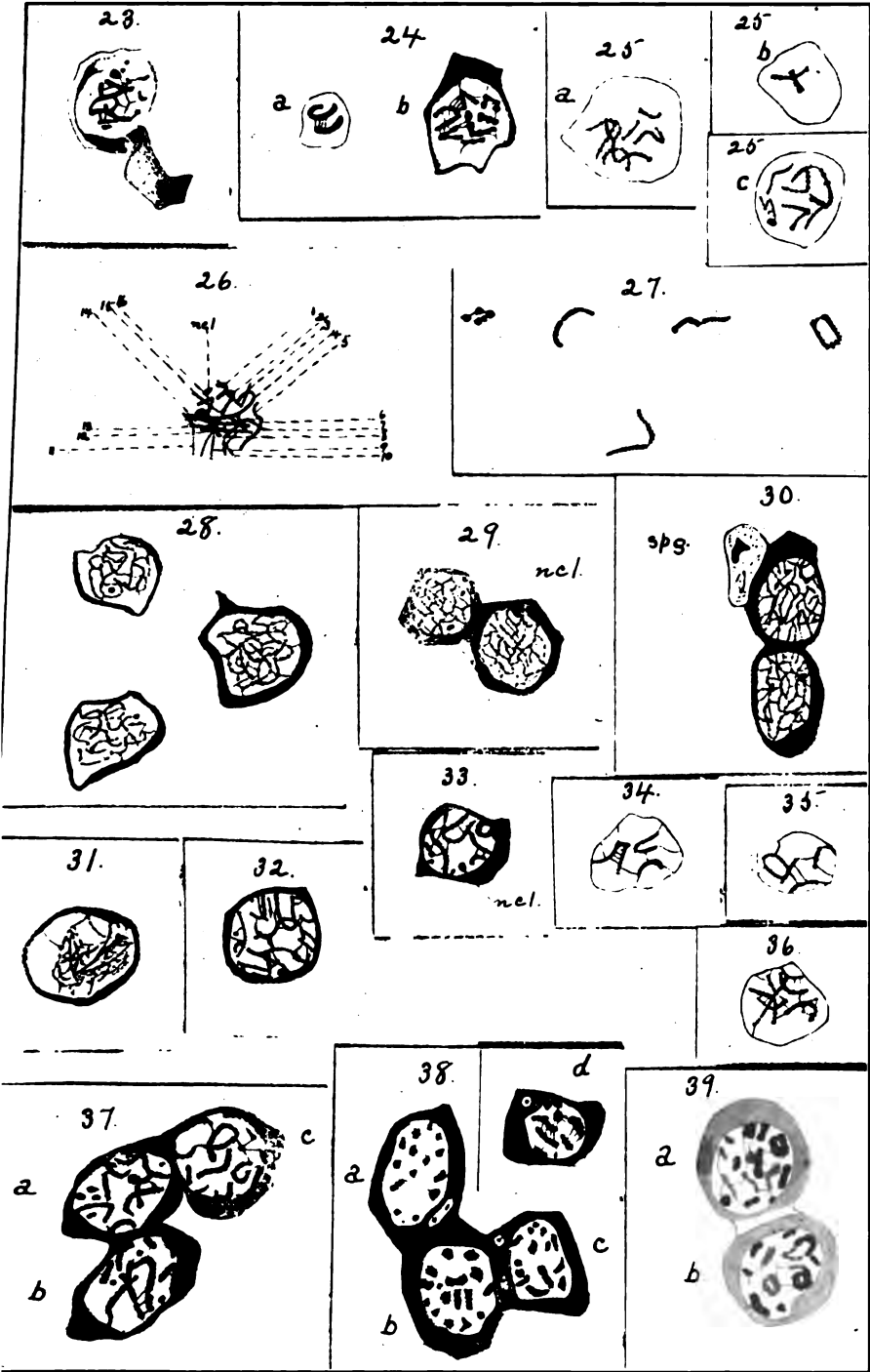






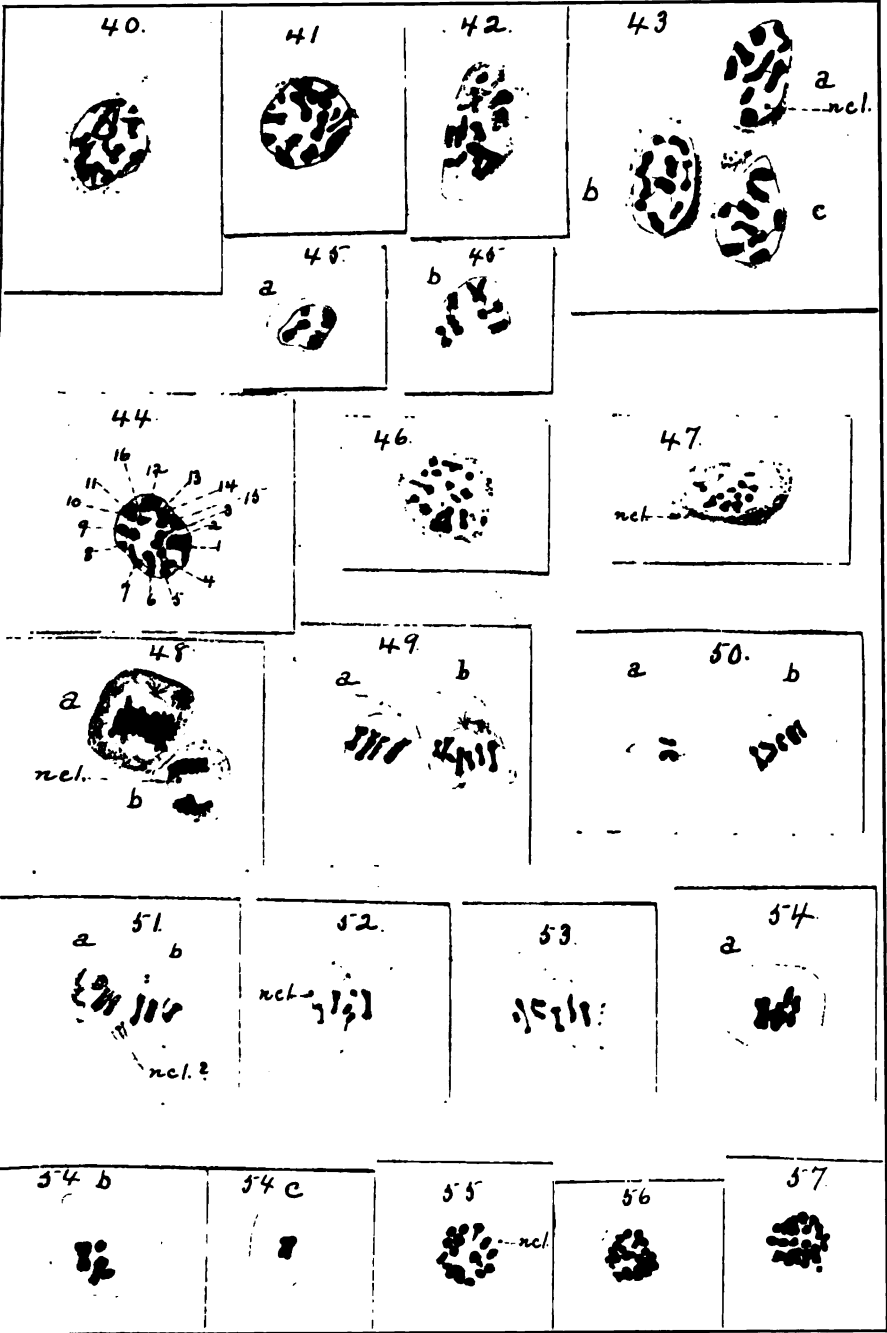






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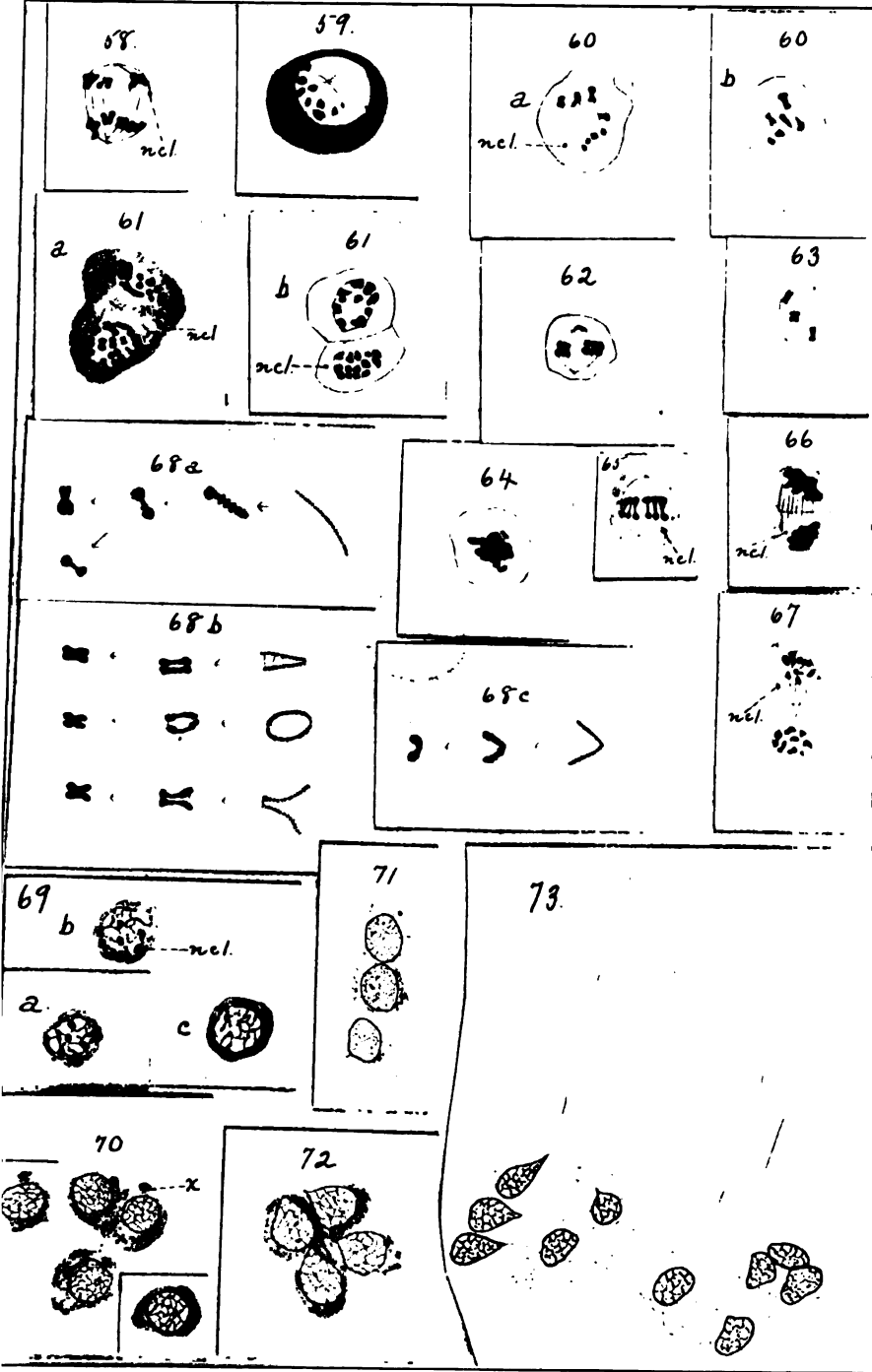




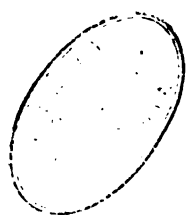
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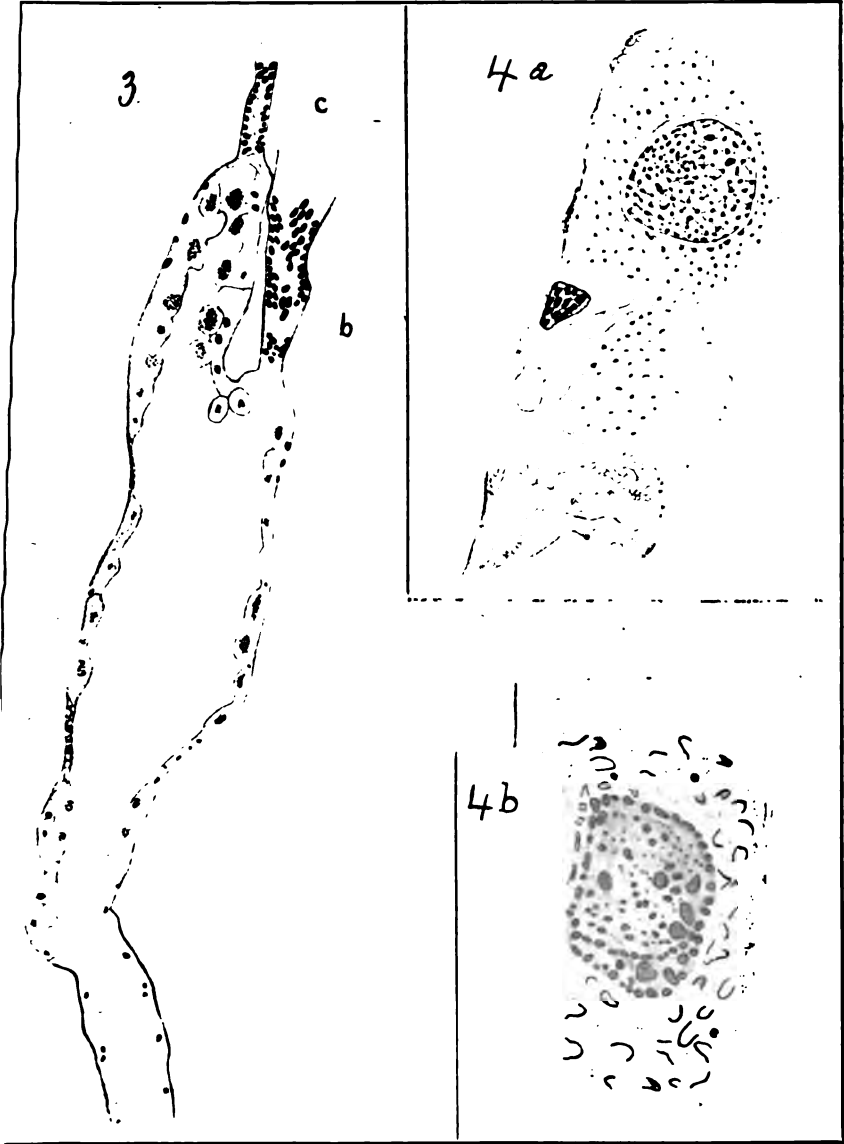




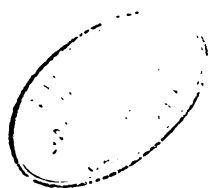


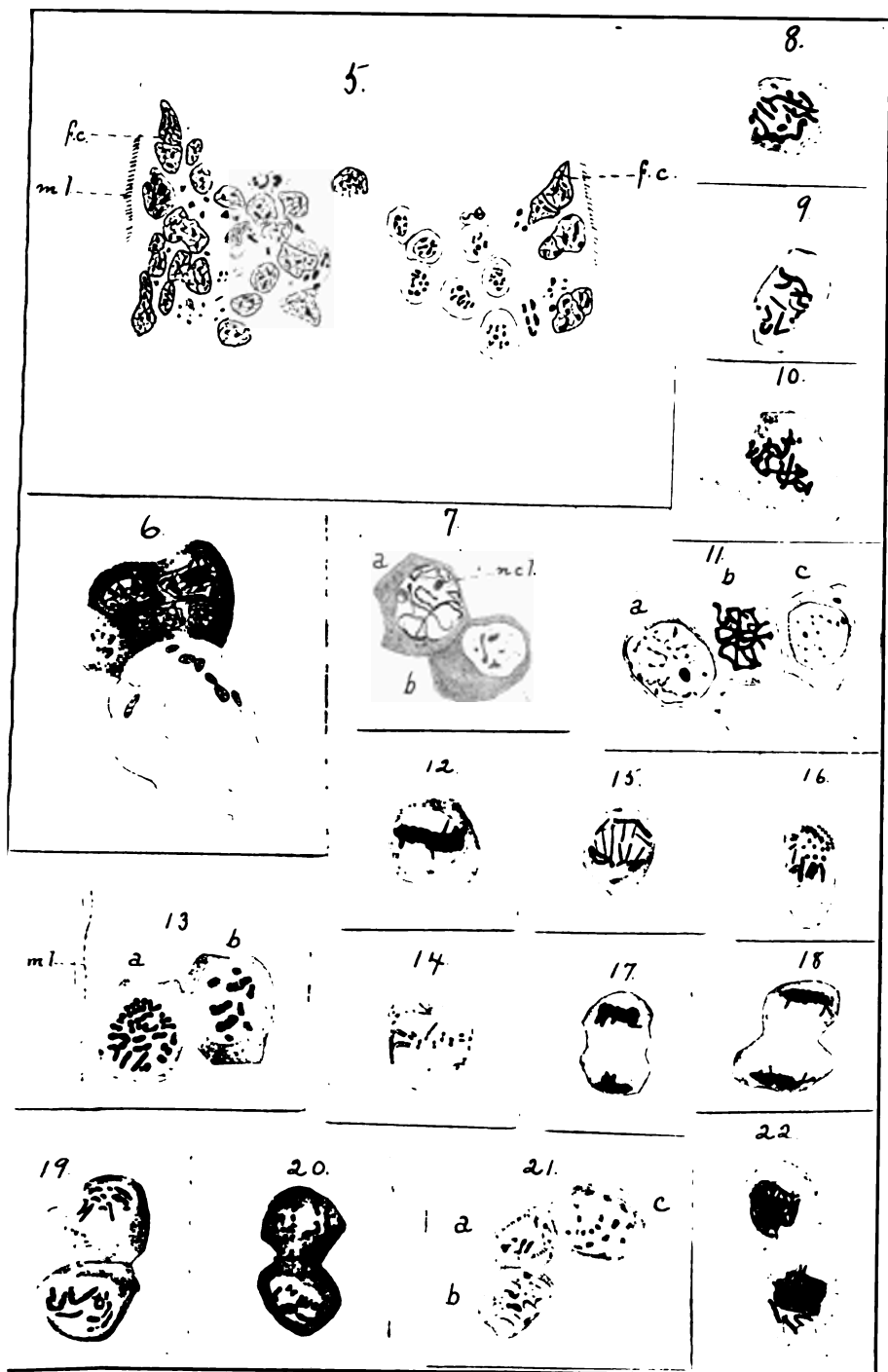
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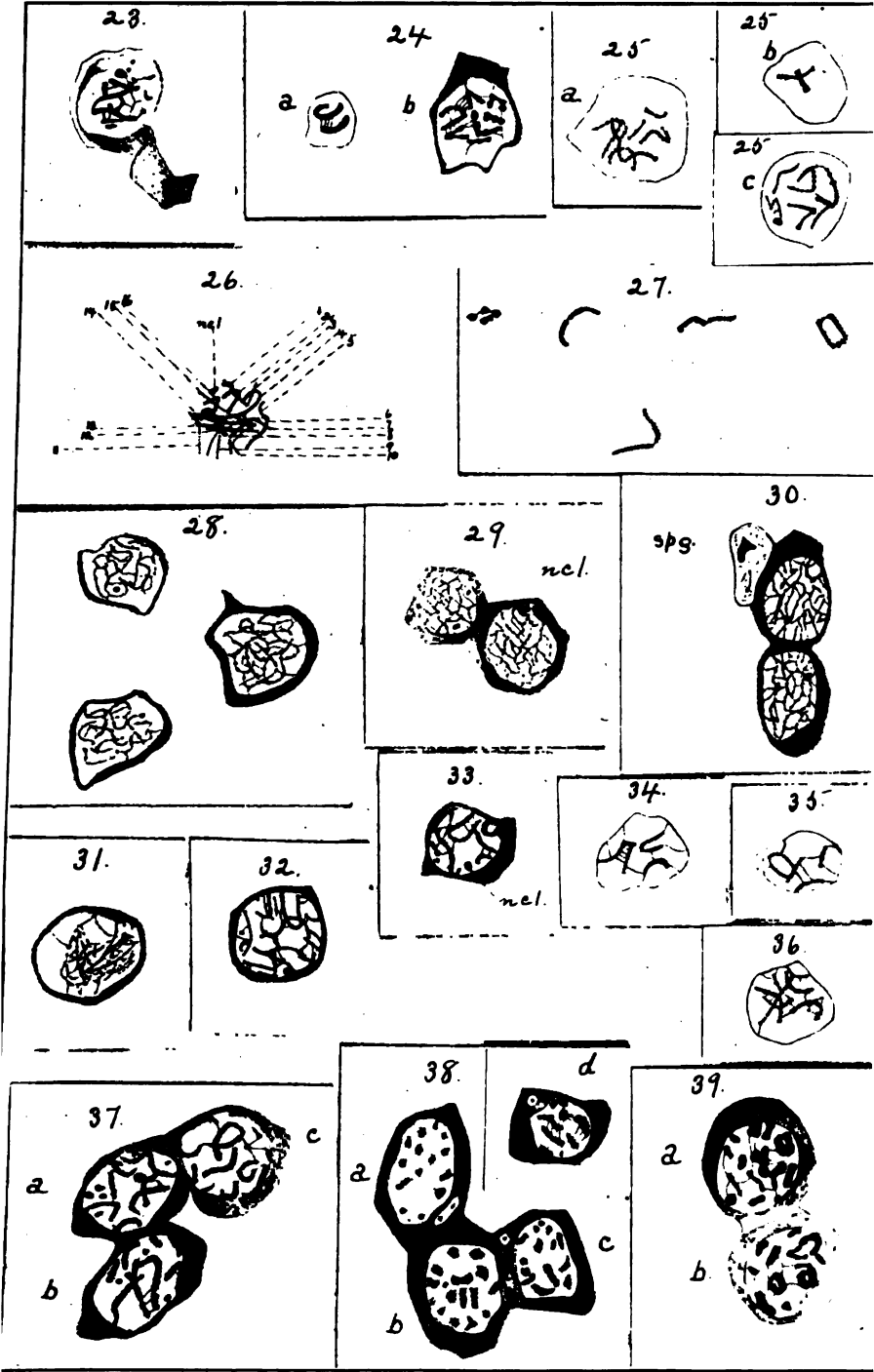


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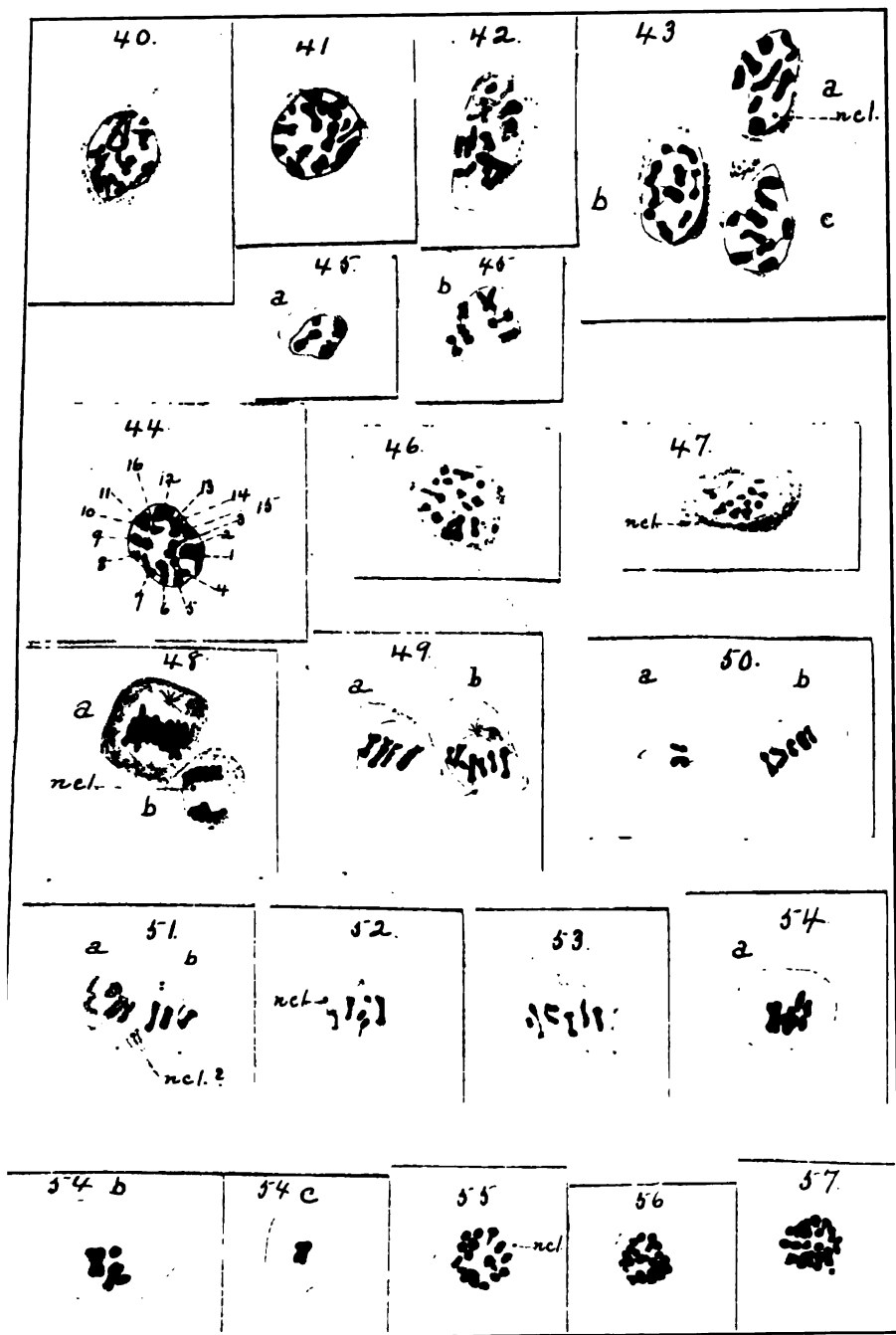




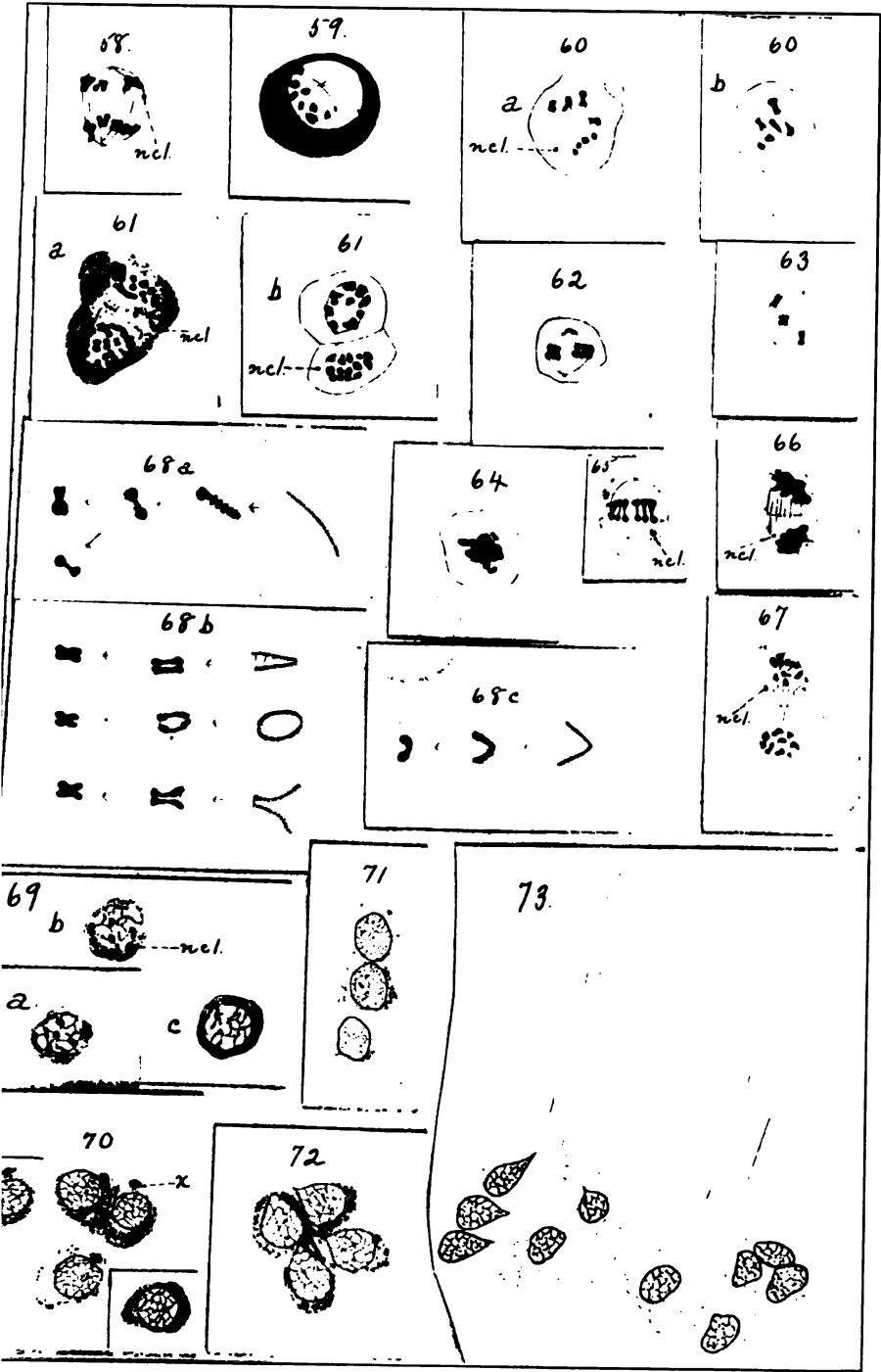






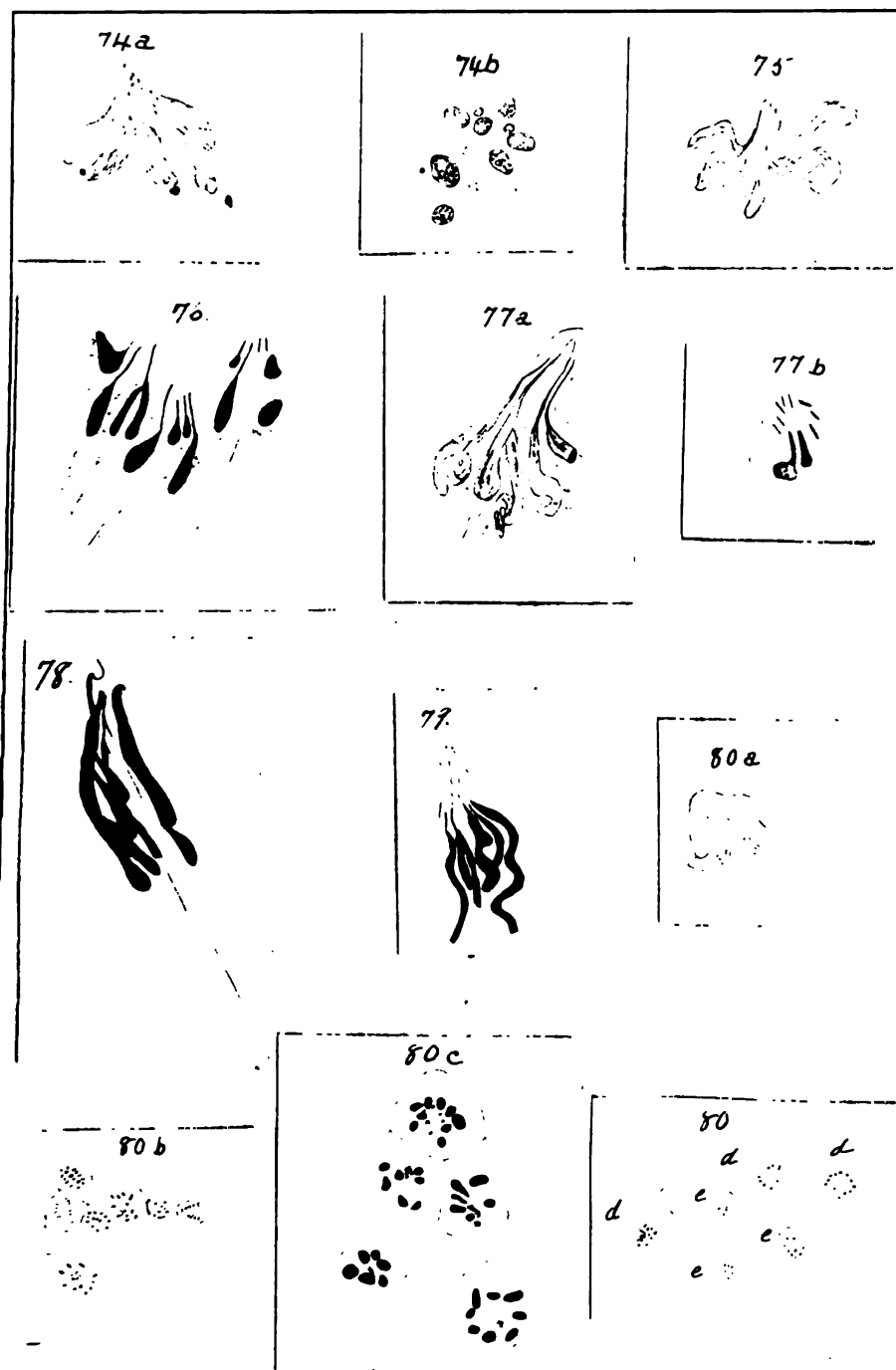




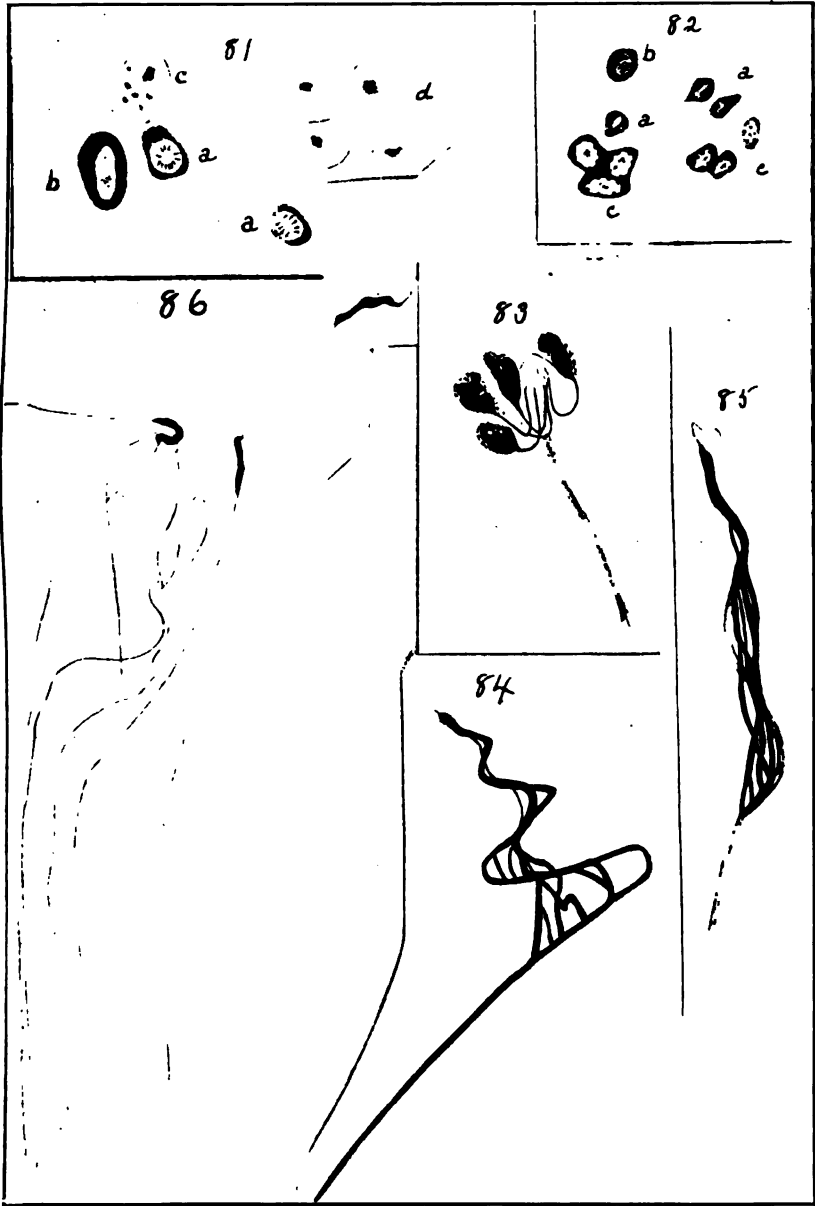


NICHOLS—SPERMATOGENESIS OF ONISCUS ASELLUS LINN.













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ORIGIN OF THE OLIGOCENE AND MIOCENE DEPOSITS  
OF THE GREAT PLAINS.

BY J. B. HATCHER.

*(Read April 3, 1902.)*

Skirting the base of the Rocky Mountains and covering the surface of the plains for some two or three hundred miles to the eastward is a series of Tertiary clays and sandstones with a combined maximum thickness of over 1700 feet. This extends from the Rio Grande in southern Texas to and beyond the northern limits of the Black Hills in South Dakota, and covers the greater portion of the plains of eastern New Mexico and Colorado, southeastern Wyoming and western Texas, Oklahoma, Kansas, Nebraska and South Dakota. Within this 1700 feet of Tertiary deposits there are a number of different horizons, which are usually quite distinct both faunally and lithologically. The more important of these were long ago differentiated and given appropriate names by Hayden, Leidy, Cope, and others. If we exclude the *Equus* beds and certain other deposits at the top, of Pliocene and Pleistocene age, and which do not fall within the limits of this paper, this entire series of rocks has been considered to belong to two formations, the White River, or Oligocene, and the Loup Fork, or Miocene. The White River, so named from a stream in northwestern Nebraska and southwestern South Dakota, where it is particularly well represented, is the lowermost, and therefore the older of these two formations. It has a maximum thickness of about 700 feet and consists for the most part of very fine and usually un laminated clays, with frequent lenses of sandstones which in places become so coarse

as to appear as conglomerates. Less frequently there are strata of limestone. These are usually only an inch or two in thickness, though occasionally attaining to as much as a foot. They are always of quite limited extent laterally.

The White River formation has been subdivided into the Titanotherium and Oreodon beds, the former at the base, the latter at the top of the series. The Titanotherium beds have a maximum thickness of about two hundred feet, and are composed of very fine, white, reddish- or greenish-colored clays with numerous lenses of sandstones and conglomerates, not faunally distinguishable, however, from the clays. The Oreodon beds, with apparently slight local unconformities, immediately overlie the Titanotherium beds. They have a maximum thickness of five hundred feet and consist of brown or pinkish-colored clays, banded but usually not laminated except at one or two horizons where distinct lamination is plainly visible. The clays of the Oreodon beds are interrupted by sandstone lenses, though less frequently than are those of the Titanotherium beds, and the sandstones of the upper series are usually of a much finer grain than are those of the lower. Toward the bottom of the Oreodon beds in the Bad Lands of South Dakota, there is a series of sandstone lenses known as the Metamynodon sandstones. These sandstones are faunally distinct from the surrounding clays. At the top of the Oreodon beds in the same region, these sandstone lenses are replaced by a second series very similar lithologically to the first, but quite distinct faunally. These upper sandstone lenses have been called the Protoceras sandstones. Their fauna differs not only from that of the lower Metamynodon sandstones, but from that of the adjoining clays as well. While the Metamynodon and Protoceras sandstones are faunally quite distinct, both from one another and from the adjoining and underlying clays, sandstones and conglomerates of the Oreodon and Titanotherium beds, they are, in so far as is at present known, of extremely local distribution. At present neither of these two series of sandstones has been recognized outside of a very limited area in the South Dakota Bad Lands. Here they appear as lenses marking the course of an ancient river channel, that in Oligocene times crossed these plains in a direction almost at right angles to the present courses of the Cheyenne and White Rivers, now the two principal streams of this immediate region. On the same horizon with the Protoceras sandstones and contemporaneous with them in

origin, there is in the South Dakota Bad Lands a series of pinkish-colored nodular clays. These clays are faunally quite distinct, both from the adjoining sandstones and the underlying clays of the lower Oreodon beds. Unlike the Matamynodon and Protoceras sandstones, this upper series of clays is of wide distribution and has been recognized in South Dakota, Nebraska, Wyoming and Colorado. Dr. W. D. Matthew, in his most excellent memoir on the *Fossil Mammals of the Tertiary of Northeastern Colorado*, has very appropriately named these clays the *Leptauchenia Beds*, from a genus of fossil mammals occurring abundantly in them.

From the above remarks it will readily appear that the White River formation may be separated faunally into three sub-equal primary divisions. These are, commencing with the lowermost, as follows:

1. *The Titanotherium Beds*, consisting of 200 feet of fine, white or greenish-colored clays with numerous intercalated lenses of sandstones and conglomerates, the latter not faunally distinguishable from the clays.

2. *The Oreodon Beds*, consisting of 300 feet of pinkish-colored, banded and frequently nodular but usually un laminated clays, with less frequent lenses of finer sandstones, faunally distinct and known as the *Matamynodon sandstones*.

3. *The Leptauchenia Beds*, consisting of 200 feet of pinkish-colored, often nodular and banded, but un laminated clays, including the *Protoceras sandstones* above referred to.

The *Loup Fork* was the name given by Cope to a series of sandstones and clays well represented in western Nebraska and Kansas. This formation has since been found to have a very wide distribution, and to extend almost uninterruptedly all along the eastern base of the Rockies from Mexico to the Missouri River. It attains its greatest development in southeastern Wyoming and northwestern Nebraska, where it has a thickness of more than 1500 feet.

The sediments of the Loup Fork formation have not been so thoroughly studied as those of the White River, and their faunal and lithological characters are consequently less perfectly known. The latest attempt at a differentiation of the various horizons within the Loup Fork is that of Darton. Chiefly by lithological characters he has divided the Loup Fork of northwestern Nebraska into three divisions. Commencing below these are:

1. *The Gering Sandstones.*—These consist of some 200 feet of laminated, massive and cross-bedded sandstones, found either conformably or unconformably overlying the White River formation at various localities in western and northwestern Nebraska. They are well shown at the mouth of Monroe Creek cañon, some five miles north of Harrison, Sioux County, Nebraska. Few fossils have been found in these sandstones.
2. *The Arikaree Sandstones.*—These consist of some 500 feet or more of light-gray, soft, massive sandstones, everywhere characterized by numerous, flattened, horizontally columnar, hard, dark-gray concretions. These concretions have an average vertical thickness of about one foot; they are frequently several yards in width and often several hundred feet in length. They have a general northwesterly and southeasterly trend. The Arikaree sandstones are especially well developed in the northern face of Pine Ridge, in Sioux County, Nebraska, and Converse County, Wyoming. In this region these sandstones may be conveniently subdivided into an upper and lower series, easily distinguishable both by faunal and lithological characters. These subdivisions in the Arikaree will be referred to and fully described later.
3. *The Ogallala Formation.*—This consists of a series of calcareous grits, loose brown sands and clays with occasional coarse conglomerates, the whole attaining to an aggregate maximum thickness of 300 feet. It is the equivalent of the *Goodnight* (Palo Duro) beds of Texas and Kansas, and is especially well developed in western Nebraska and Kansas, between the Platte and Arkansas Rivers. It is usually referred to the Pliocene, but a portion, or all of it, may yet prove to belong to the Miocene.

Returning to the Arikaree formation, I have already remarked that in Sioux County, Nebraska, and Converse County, Wyoming, it is lithologically and faunally divisible into two easily distinguishable horizons. Commencing below, these may be named and characterized as follows:

1. *The Monroe Creek Beds.*—These are well shown in the northern face of Pine Ridge, at the mouth of the Monroe Creek cañon, five miles north of Harrison, Nebraska, where they overlie the Gering sandstones, and are composed of some

300 feet of very light-colored, fine-grained, not very hard, but firm and massive sandstones. On account of their usually barren nature they have been neglected by collectors, and very little is known concerning their fauna beyond the fact that toward the top they contain *Promerycochærus*. They decrease in thickness very rapidly to the eastward and increase to the westward.

2. *The Harrison Beds*.—These are well shown in the bluffs of all the small streams that head near the summit of Pine Ridge, in the vicinity of Harrison, Nebraska. They are also known to cover a considerable area to the east, west and south of that village, extending well into the State of Wyoming. They are composed of about 200 feet of fine-grained, rather incoherent sandstones, permeated by great numbers of siliceous tubes arranged vertically rather than horizontally. They are further characterized by the presence, often in the greatest abundance, of those peculiar and interesting, but as yet not well understood, fossils known as *Dæmonelix*, and by a considerable variety of fossil mammals belonging to characteristic Miocene genera. They immediately and conformably overlie the Monroe Creek beds and pass insensibly into them. Above these come :

*The Nebraska Beds*, of Scott.—These consist of a series of buff-colored sandstones of varying degrees of hardness and unknown thickness, with occasional layers of siliceous (not calcareous) grits, which protrude as hard, indurated or shelving masses from the underlying and overlying softer materials. These beds are rich in vertebrate fossils, such genera as *Cosoryx*, *Protolabis*, *Cyclopidius* and *Merycochærus* predominating. They are represented at various localities along the Niobrara River, south of Harrison, Nebraska, where they are of unknown thickness and immediately overlie the Harrison beds. Toward the south they pass beneath the Ogalalla formation.

According to the above classification all the Miocene deposits of this region are referred to the Loup Fork, notwithstanding their great thickness and, in certain localities at least, their apparent conformity with the underlying Oligocene deposits, and without regard for the fact that throughout the lowermost 500 to 1500 feet of these sediments there is as yet practically no paleontological evidence as

to their exact age and correlation. Considering the absence of such direct paleontological evidence, it may be just as well to continue to refer this entire series to the Loup Fork; but I believe it more probable that the Gering sandstones, and perhaps a portion at least of the overlying Monroe Creek beds, will prove eventually to belong to the John Day rather than the Loup Fork. The maximum thickness of these two formations in Converse County, Wyoming, can hardly be less than 1500 feet, and almost nothing is known of the fauna of this entire series. Although for the most part quite barren of fossils, it would seem that somewhere throughout its great vertical and lateral extent there must be fossiliferous horizons, and that within these representatives of the John Day fauna will yet be found. The paucity of these beds as compared with the great wealth of fossils in the underlying and overlying deposits, have heretofore caused them to be almost totally neglected by collectors. I believe a better classification of these beds would be obtained by making Darton's Arikaree coördinate with the Loup Fork, including within it the Gering sandstones and Monroe Creek beds, correlating it provisionally with the John Day.

The following table is submitted as expressing the present author's views as to the proper classification of the Oligocene and Miocene deposits of this region. It is based on our present knowledge of the faunal and lithological characters of the various horizons as they have been determined, chiefly in northwestern Nebraska and southwestern South Dakota, where these deposits are best represented and have been most thoroughly studied.

TABLE OF OLIGOCENE AND MIOCENE FORMATIONS OF WESTERN PLAINS.

Miocene.	{	Loup Fork.	{	Goodnight = Palo Duro = Ogalalla.
				Nebraska = Upper Deep River.
				Harrison = Hiatus between Lower and Upper Deep River.
		Arikaree.	{	Monroe Creek = Upper John Day and Lower Deep River.
				Gering Sandstones = Lower John Day.
Oligocene = White River.	{		{	Leptauchenia Clays, including Protoceras Sandstones.
				Oreodon Clays, including Metamynodon Sandstones.
				Titanotherium Sandstones and Clays.

The writer is well aware that the above correlation of the Gering and Monroe Creek sandstones is open to criticism, as being at present inadequately substantiated by direct paleontological evidence. However, it should be remembered that on the other hand there are no direct paleontological evidences against such correlation, and that since sedimentation seems to have been continuous at certain localities in this region, from the base of the White River to the top of the Loup Fork, the John Day should be represented somewhere in the series, and that the lithological sequence, as well as the faunas of the overlying and underlying rocks, point to the Gering and Monroe Creek sandstones as the logical representatives of the John Day formation in this region.

#### ORIGIN OF THE DEPOSITS.

Until very recently the sediments of this entire series of deposits have been very generally considered as of lacustrine origin, and the boundaries of these supposed great Oligocene and Miocene lakes have been set forth in text-books and scattered papers, and especially in the classroom lectures on the subject at our various universities, with a preciseness only surpassed by that of the modern geographer when dealing with existing lakes.

The earlier writers, including David Dale Owen, King, Hayden, Leidy, Cope, Marsh and others, were always accustomed to speak of these deposits as lacustrine, and they are at present so considered by many authorities. Recently, however, their lacustrine origin has been rejected, at least partially, by a considerable number of competent observers, several of whom have had most excellent opportunities for studying them. This is especially true of the upper or Loup Fork series of deposits, which has now come very generally to be considered as of combined lacustrine, fluvatile, flood-plain and æolian origin, instead of as having been laid down over the bottom of a great and continuous body of water, as was formerly supposed.

With regard to the origin of the underlying White River series, however, it has been different; and with a few exceptions these deposits are still regarded as of lacustrine origin. Dr. W. D. Matthew, in an article entitled "Is the White River Tertiary an *Æolian* Formation?" published in the *American Naturalist*, for May, 1899, was the first to seriously question the lacustrine origin of these deposits. In his "Fossil Mammals of the Tertiary of



Northeastern Colorado," published as Part VII of Vol. I of the *Memoirs of the American Museum of Natural History*, Dr. Matthew has set forth additional facts in favor of his æolian theory as to the origin of the deposits, which, if not furnishing conclusive evidence as to the correctness of his theory, at least make it very clear that the lacustrine theory is alone unable to explain many well-known facts relating to the nature of these deposits and the distribution, condition and nature of the animal remains found in them. W. D. Johnson, in his paper on "The High Plains and their Utilization," published in the Twenty-first Annual Report of the United States Geological Survey, has entirely ignored the lacustrine theory of the origin of any of the Tertiary deposits of the plains, holding that they are of fluvial and flood-plain origin, while Dr. J. C. Merriam, in a recent paper on "The Geology of the John Day Basin," rejects the lacustrine theory of the origin of those deposits, which had previously remained unquestioned. The above are the leading authorities among those who have questioned the lake theory as to the origin of these beds. On the other side the lacustrine origin of the rocks of the White River series, at least, has been maintained by Todd, Scott, Darton and others, though none of these authorities have thought it worth while to support their contentions by the production of any considerable direct or indirect evidence bearing on the case. Like the earlier writers they have, almost without exception, set forth their views as if they were well-established facts and beyond question or criticism. The following quotation from Scott is a fair example. In speaking of the Oligocene series, on page 507 of his *Introduction to Geology*, he says: "But in the interior regions are extensive fresh-water deposits which clearly should be referred to it and which form the White River stage. The largest body of water of this time occupied northeastern Colorado, southeastern Wyoming, much of western Nebraska and South Dakota." But the limits of this supposed Oligocene lake have lately been greatly extended by Darton, who has contended that it covered all of eastern and central Wyoming, and a considerable portion of Montana and North Dakota as well; so that one is at a loss to understand where lived the terrestrial mammals and reptiles whose remains are now found in such abundance in the deposits.

The lacustrine theory had its origin in the until recently universally accepted idea that all sedimentary rocks showing stratification

or bedding were deposited in either marine or fresh waters. Moreover the color-bands exhibited, more especially by the clays of the White River series, have been very generally mistaken for examples of stratification and lamination, while true lamination in the clays of this series is rare and usually of very limited extent both vertically and horizontally.

Dr. Matthew, in his *Memoir* already referred to, has set forth in very clear and concise language the principal stratigraphic and paleontologic evidences against the lacustrine theory as observed by him for these deposits in northeastern Colorado. It will be the chief purpose of the succeeding pages of this paper to extend these observations into southeastern Wyoming and western Nebraska and South Dakota, and to record some additional facts relating to the stratigraphy, paleontology and paleobotany of the beds, with especial reference to their bearing upon the origin and mode of deposition of the latter.

Matthew has already called attention to the physical and topographical difficulties, as well as to the lack of terraces and of certain stratigraphical characters which should exist if these deposits had their origin in a body of fresh water of a size comparable with that outlined by Scott. These difficulties, already serious, are only augmented by the increased dimensions of this lake proposed by Darton. If we confine it, however, to the much more restricted limits given by Dr. Scott we still have a lake of very considerable dimensions, greatly exceeding in size those of any fresh-water lake of modern times, with no barrier to the east or south to retain its waters, without recognizable terraces about its shores, and with a distribution of materials and of remains of fresh water, and of terrestrial plants and animals which are at least difficult, if not impossible, of explanation by the assumption of the presence of a great lake.

#### CHARACTER OF THE MATERIALS IN THE WHITE RIVER SERIES.

We have already observed, while discussing the classification of the White River beds, the presence in them of frequent lenses of sandstones and conglomerates. These sandstone and conglomerate lenses are not arranged concentrically at varying altitudes about the margins of this supposed great lake, but extend as greatly elongated and narrow lenses far out into the very centre of the region which this lake has been supposed to have occupied. They occur at all

horizons, show frequent examples of cross-bedding and their irregular course, as well as the spheroidal shape of the pebbles they contain,<sup>1</sup> and the increased fineness of the materials of which they are composed as one proceeds from the margin toward the interior, are all characters strongly suggesting that they were deposited in river channels. Moreover, the materials of these sandstone and conglomerate lenses are not only coarser about the western borders of the beds, but the lenses are far more numerous in that region. Toward the interior these lenses converge and unite without spreading out laterally, so that in the region lying east of the Black Hills in South Dakota, at a distance of fifty to seventy-five miles from the mountains, the sandstones are finer, less frequent and are separated by greater areas of fine clays, just as the streams of the present day unite and become fewer in number as we proceed farther from their sources.

The *Metamynodon* and *Protoceras* sandstones, as well as certain intermediate and underlying sandstones, present many evidences, like those just enumerated, which strongly suggest that they were deposited in river channels. Taking the *Protoceras* sandstones as the most favorable example, owing to the greater extent to which they have been exposed by the subsequent erosion of the overlying sediments, they are seen to extend as a series of narrow elongated lenses from the summit of the Cheyenne and White River divide for several miles to the southward of the last-mentioned stream, where they pass beneath more recent deposits. Throughout their entire extent they exhibit frequent examples of cross-bedding, while the sands become finer and the channels fewer in number and broader and deeper as one goes southward toward and across White River. That they have been removed by erosion over considerable areas lying between their present limits and the Black Hills is evident. At the summit of the Cheyenne and White River divide there are several of these sandstone lenses at approximately the same horizon. These bear many evidences of having been deposited in the channels of small streams or rivers pertaining to a single drainage system, which had its source somewhere in the

<sup>1</sup> A conglomerate accumulated by a running stream can usually be distinguished very readily from one formed on the beach of a lake or sea, by the shape of the contained pebbles. In the first instance the pebbles have been reduced to irregular spheroids by the rolling motion to which they have been submitted by the current. In the second they are more generally flattened disks.

present region of the Black Hills and was tributary to a much larger river coming from the southwest. These sandstone lenses appear to converge and unite as one proceeds toward White River, like the tributaries of recent streams. I am at a loss to understand how these greatly elongated sandstone lenses, confined laterally to at most only a few hundred yards in breadth, and necessitating the presence of strong currents, could have been deposited in the bottom of a great lake. For they appear not only to extend quite across the entire region which this lake has been supposed to have occupied, but these or very similar sandstones are found at intervals throughout the entire vertical and lateral extent of the beds, although as one recedes eastward from the western border they become less frequent and of finer grain. Such difficulties as those just mentioned, together with others to be referred to later, long ago demonstrated to the present writer the untenable nature of the lake theory as to the origin of these deposits.

If these beds had their origin in a great lake it may very naturally be asked, Where are the remains of the aquatic fauna which a lake of such dimensions may very reasonably be supposed to have contained? The reply has been made, and will be forthcoming from advocates of the lake theory, that the waters of this great lake were of such a saline or alkaline nature that it was incapable of supporting life. Hence the absence of the remains of aquatic animals. But I shall show presently that such bodies of water as did exist in this region during the deposition of these beds were not only not of such a nature, but that they were eminently fitted for the support of aquatic life and did in fact support such life, both plant and animal, in great abundance.

Again, if a lake deposit, how did the remains of terrestrial mammals and reptiles receive their present distribution throughout these beds? It has been maintained by advocates of the lake theory that the fine-grained, banded clays were deposited in the deep and quiet waters of the lake and the sandstone and conglomerate lenses along the shores and about the mouths of tributary streams, while the preservation and distribution of the remains of terrestrial mammals and reptiles was accomplished by the drifting about in the lake of dead carcasses brought down by the tributary streams. Such a theory requires conditions which are not only quite unreasonable but unparalleled elsewhere, both in the deposits of the lakes and seas of the present day and those of past geological epochs. Fur-

thermore it not only does not account for but is actually opposed to the present distribution of the fossils. If, as we are told, the fine clays were deposited over the deeper and quieter waters of the lake and the sandstones and conglomerates about the mouths of rivers and along the shores, why, I may ask, is it that the former contain absolutely by thousands the remains of giant land-tortoises, while these if not entirely absent are conspicuously rare in the sandstones, while the few examples of *Trionyx*, an aquatic turtle, have, in so far as I know, all been recovered from the sandstones? I have myself collected a number of these latter from the sandstones. If the land-tortoises were brought into the lake by the rivers, ought we not to expect that their remains would be found in at least as great an abundance in the sandstones as in the clays? Again, while it is quite possible to conceive of even a huge animal of such elephantine size as was *Titanotherium* as having met death by drowning or otherwise in or near some stream, where the dead body inflated by gases would be carried out by the current into the waters of the lake to sink later, allowing the bones to be preserved in the clays at the bottom, it is difficult to understand how such examples could be other than exceptional, and it is totally incapable of explaining the present distribution and abundance of such bones. In such a case as that just supposed it seems quite probable that once decomposition had proceeded far enough to weaken the body walls sufficiently to permit of the escape of the confined gases, the carcass would sink to the bottom and the bones of the skeleton be preserved in approximately their normal position relative to one another, just as are the skeletons of marine reptiles in the chalk beds of western Kansas or at Lyme-Regis in England. If this were the case we should expect to find complete skeletons at least fairly common, but they are in fact exceptionally rare, and for every even approximately complete skeleton to be found there are scores of isolated skulls and other bones. Taking *Titanotherium* as an example, I have myself collected nearly two hundred skulls of this animal, while the number of fairly complete skeletons at present known may be counted on the fingers of one hand. What is true of this animal applies likewise to the others found in the beds.

But, it will be asked, if the lake theory is so objectionable, why do you not offer a better? Such has already been done by Matthew, and it is the purpose of the present paper to support

in a somewhat modified form the theory advanced by him, extending his observations and adding certain additional facts observed by the present writer and bearing directly upon the subject.

Matthew's theory as to the origin of these deposits may best be described in his own language. Speaking of the conditions attending the deposition of these beds, he says: "The nature of the organic remains, where such have been found, seem to definitely negative the idea of any vast lake, and to favor less the theory of a series of lagoons and swamps than that of a broad, open and comparatively level plain, with shallow, probably wooded, rivers meandering over parts of it and deposits partly or chiefly brought by rivers, but in large part redistributed over the higher sodded grassland by the agency of the wind." With most of the principal features of this theory as applied by its author the present writer is in accord. I believe, however, that the materials on the whole partake more of the nature of fluvial and flood-plain deposits than of those characteristic of prairie loess.

#### PALEONTOLOGICAL EVIDENCES.

The distribution, state of preservation, nature and character of the animal and plant remains found in the clays and sandstones, as well as the distribution of the latter, absolutely preclude the possibility of their having been deposited in a vast lake and favor the presence of streams meandering through low, broad, level, open or wooded valleys subjected in part at least to frequent inundations, conditions very similar to those at present prevailing in the interior of South America, about the headwaters of the Orinoco, the Amazon and the Paraguay and Parana Rivers.

Now it is evident that if such conditions prevailed in this region during the deposition of the White River beds there should remain certain evidences concerning it, such as filled-in river channels and small lagoons with their characteristic deposits and remains of the animal and vegetable life peculiar to each. Moreover some indication at least of the forests should remain and be found somewhere in this vast region. With these and many other points constantly in mind the writer passed a considerable portion of the seasons of 1900 and 1901 in exploring these deposits. Particular attention was given to ascertaining whether or not they contained an aquatic fauna and flora. The sandstone lenses were especially examined

with reference to this, for whether the deposits as a whole were of lacustrine origin or not, there could be little doubt as to the aqueous origin of the sandstones. Though for the most part remarkably barren of aquatic life, remains of *Trionyx*, fishes and crocodiles were found, and in one locality the casts of unios were observed in great numbers. A search in the clays of the Titanotherium and overlying Oreodon beds was rewarded with greater success, for numerous thin layers of limestone, varying in thickness from a fraction of an inch to a foot or more and always of limited areal extent, were discovered at many horizons rich in the remains of fresh-water plants and mollusca, such characteristically shallow-water forms as *Chara*, *Limnæa*, *Physa* and *Planorbis* occurring in the greatest abundance. I have submitted these mollusca to Drs. Dall, Pilsbry and Stanton, and all have assured me that they belong to species inhabiting swamps and small ponds, and could not have lived in the midst of a great lake; while Dr. Knowlton, who has examined the plants, finds in great abundance the stems and seeds of *Chara*, which, as all know, is distinctly an inhabitant of small springs, shallow ponds and brooks. The presence of these thin limestone layers with such characteristically swamp plants and mollusca as are *Chara* and *Physa* at various horizons throughout the White River series, and in the very midst of the region which was supposed to have been occupied by a great lake, and intercalated with the clays which advocates of the lake theory maintain were deposited in the deep and quiet waters, would appear to preclude the possibility of the existence of such a lake in White River times. Moreover remains of forests were found at several places and at different horizons throughout these beds. At various localities in the Hat Creek basin in Sioux County, Nebraska, I discovered remains of the silicified trunks of trees and seeds belonging especially to *Hickoria* and *Celtis*. These were found at various horizons from the middle Titanotherium beds to the very top of the Loup Fork. And in South Dakota, some twelve miles north of White River, opposite the mouth of Corn Creek, I discovered the remains of a no inconsiderable forest. Here in the upper Titanotherium beds and lower Oreodon beds there occur, actually by hundreds, the silicified stumps and partially decayed trunks of trees, weathering out of the fine clays of these deposits. It was noticeable that only the knots and lower stumps had been preserved. Nothing like complete trunks were to be observed, and the entire



aspect was that of the remains of a dead and decayed forest on the margin of some stream, where only the less destructible knots and stumps would endure sufficiently long to be finally covered up and preserved. In this same region there were discernible certain strata which seemed to indicate that during the deposition of these beds there had been at several horizons an accumulation of vegetable mould or humus, and on Dry Creek, some five miles northeast of Chadron, in Dawes County, Nebraska, I observed near the base of the *Oreodon* beds a stratum of some two feet of dark-colored humus, clearly indicating that this region had not been occupied by a great lake while this stratum was being deposited.

The advocates of the lake theory have always maintained that the fine clays of the *Oreodon* and *Titanotherium* beds were deposited in the deep and quiet waters of the lake, explaining the absence of the remains of an aquatic fauna, such as a lake of so great dimensions might in all reason be expected to maintain, on the theory that this lake was of such a saline or alkaline nature as to render its waters uninhabitable by crocodiles, turtles and fresh-water fishes. But I have shown that the remains of such animals do occur, though sparsely, wherever there is evidence of sufficient water to maintain them. The character and abundance of the mollusca and aquatic plants found in the thin limestone lenses throughout the clays show that such bodies of water as were present, although limited in area, were eminently well adapted to fresh-water life. The great abundance of land-tortoises in the clays and their almost complete absence in the sandstones is very strong if not positive evidence that the former were not deposited in the bottom of a great lake, for I do not believe that any one will assume to explain the present distribution of the remains of these land-turtles on the lake theory. After a careful consideration of the materials composing the White River deposits and the distribution and character of the fossils throughout the sandstones, conglomerates, clays and limestones, the present writer believes that the sandstones, conglomerates and a portion of the clays were deposited in river channels, while the limestone lenses, so rich in the remains of aquatic plants and mollusks, originated in shallow ponds and lakes scattered over the higher table-lands and the broad flood-plains of the rivers, where for the most part the finer clays were deposited by occasional inundations and through the agency of the winds. Such a theory as to the origin of the White River



beds appears to the writer not only to be in harmony with all the observed facts, but moreover the conditions which it presupposes are paralleled by existing conditions in other parts of the earth's surface.

The following description of the conditions at present prevailing about the sources of the Parana and Paraguay Rivers in central South America has been furnished me by Mr. H. H. Smith, who has spent several years in that region and has had exceptional advantages for studying the physical conditions that obtain about the headwaters of these streams and their tributaries. He says:

"Ascending the River Paraguay from Asuncion, the river hugs the higher lands of the eastern or Paraguay side or is separated from them by strips of alluvium. On the western or Chaco side the ground is always low and flat, hardly above reach of the annual freshets and proportionally a little lower toward the north. During the rains water covers large spaces of these flatlands, but it does not come from the river and is gradually drained away after the rains cease. Above the mouths of the Vermejo the Chaco bank is at first covered with low forest; farther north great areas have a scattered growth of Carandá palms with grass beneath, but with no other vegetation. The Chaco plains extend far inland to the table-land of Bolivia, which is said to fall abruptly to the plain.

"At latitude  $21^{\circ} 26' 40''$  S. the river flows through a narrow pass, the *Fecho dos Morros*, between two rocky hills. The hill on the eastern side is connected by high ground with the Brazilian table-land. That on the western side appears from the river to form one of a number of isolated hills which rise from the Chaco plain. It may be, however, that there is rocky ground extending westward to the Bolivian table-land, and perhaps connected with the Corumbá hills. This region, however, is practically unexplored, and nothing definite can be said about it. If there is a connection with the Bolivian highland, the basin of the upper Paraguay is completely enclosed like a lake, with only the narrow outlet at the *Fecho dos Morros*. If the hill on the western side is isolated, it is probably one of a chain which extends inland and imperfectly closes the Paraguay basin on this side.

"Above the *Fecho dos Morros* the character of the vegetation changes; the Carandá palms disappear; there is left only open grassland, with lines of bushes here and there and often a thin

fringe of forest on the river bank. The river at the flood season covers these lands almost entirely. It must be remembered that the upper Paraguay rises about thirty feet annually.

"All the flatlands above the Fecho dos Morros to Villa Maria—over four hundred miles in a direct line—are subject to river floods, and these are deepest toward the north. The width of the flood-plain at the mouth of the São Lourenço can hardly be less than one hundred and fifty miles from the rocky lands on the east to the base of the Serra dos Dourados. The whole region is a labyrinth of lakes, ponds, swamps, channels and islands in a grassy plain, the only forest being near the river. I had a fine view of this plain from the foothills of the Dourados; even the flood-plains of the Amazon cannot compare with it in its tangle of land, water and marshes. Only the most experienced canoeman can thread his way through it; generally travelers trust to the Guató Indians, who are the only inhabitants of the region and literally live in canoes. Castelnau was lost there and only found the river channel with great difficulty. We were lost or partly lost for a few hours, though we had three experienced hands.

"This is the region called Lake Xaraés, or Charaés, by the old explorers; Brazilians called it the Pantanaes, literally The Marshes. Even at low water at least one-fourth of it is flooded: when the river is at its highest the whole plain is a vast lake covered with floating grass and weeds; it is possible to pass almost straight across it in a canoe, though with great difficulty. Only a few islands remain here and there; jaguars, deer and other animals take refuge on them, and they are favorite hunting grounds of the Guatós.

"The rainy season is from October to April, the heaviest rains being toward the last; the small rivers from the highlands are flooded in March and April, and pour their waters over the flood-plain. But it takes a long time for these waters to spread over the plain. Consequently the highest waters on the plain are in July and August. Then they gradually drain away through the Fecho dos Morros, and the lowest waters are found about February.

"The eastern and northern sides of the flood-plains are bordered by low rocky lands which extend for a few miles inland: then they rise precipitously 1500 or 1800 feet to the Brazilian plateau. The

line of precipices forming the plateau may be traced from Villa Maria to near Miranda.

"On the Dourados side the case is different. Long bays of the flood-plain run back among the hills and often contain lakes of considerable size. The Dourados chain itself is narrow and on the other side are more floodlands, the region called "*Ceo e Terra*" by the Brazilians. The Brazilian-Bolivian Boundary Commission tried to pass over this land but had to turn back.

"The Paraguayan flood-plains are connected with the *Ceo e Terra* region by several strips which cut the Dourados chain. Hence the Dourados are like a chain of islands.

"A narrow neck of rocky but low land divides the Paraguayan flood-plain from similar plains in the Guaporé; those on the Guaporé are continuous to the junction of the Madeira where there are rapids; beyond that a flood-plain extends to the Amazon, broadening out. The Amazonian plain is connected in much the same way with the Orinoco. The Orinoco, Amazon and Paraguay are like each other in their flood-plains, which broaden out as we ascend the rivers.

"Except for a single break at the Fecho dos Morros (which may not be a continuous wall) a great plain stretches from Villa Maria to Rosario and beyond. The Xaraés, Chaco and Pampa differ only in their relations to the river floods. The pampas are above reach of the floods; the Chaco plains are also above the floods, but so low that the water drains off slowly; the Xaraés are covered at high water. The Paraguay and its continuation, the Paraná, cut deeper and deeper into the plains as they flow southward, hence the differences in physical features, which are more apparent than real."

From the above description it will be seen that the flood-plain of the Paraguay at the mouth of the São Lourenço has a width of one hundred and fifty miles and that it broadens as we ascend the river. It is a well-known fact, as stated by Mr. Smith, that the flood-plains of the upper Paraguay, Amazon and Orinoco Rivers are confluent, and that a vast region about the headwaters of those streams possesses physical conditions in every way similar to those just described as obtaining over the flood-plains of the upper Paraguay. Here it appears to the present writer we have a region of equal or greater area than that occupied by the Oligocene and Miocene deposits of our Western plains, with all the physical

conditions necessary for the deposition and present distribution of the sandstones, clays and conglomerates, together with the preservation of remains of the faunas characteristic of each.

Many have noticed and Prof. J. E. Todd has recorded the presence of great deposits of bones at various localities in the White River beds. He describes them as literally covering the ground in places where they have weathered out over areas frequently of more than an acre in extent. It is not only difficult, but I think impossible to account for these accumulations of bones of terrestrial animals at the bottom and in the very middle of a great lake. Since the surrounding clays are usually almost destitute of bones, it is difficult to understand how the dead carcasses of so many animals were driven or drawn as by a magnet to so limited an area. Accepting the other theory, however, we have seen how during the rainy season the deer, tapirs and other animals are driven to the islands over the flood-plains of the great South American rivers. Since in exceptionally high freshets the lower of these islands become submerged it is not difficult to understand how great numbers of these animals must annually perish, and indeed it is a well-known fact that frequently great numbers of them are caught on low islands and, driven by the rising waters to more limited confines, they are finally all drowned when the island becomes entirely submerged. To such or similar conditions the great deposits of bones in the Oligocene and Miocene deposits of the West may owe their origin. I have frequently observed these deposits, though not covering so great an area as that recorded by Todd, and I have always without exception noted that in the Oligocene beds they occurred in the very fine clays, while in the upper or Miocene deposits they occur in the finer sandstones. Although bones are fairly abundant in the sandstones of all these series of beds, I never observed these extremely rich deposits in the coarse sandstones or conglomerates.

The above facts, together with those brought forward by Dr. Matthew, have driven me, contrary to my earlier opinion, to reject the theory of a great lake and accept that of small lakes, flood-plains, river channels and higher grass-covered pampas as the conditions prevailing over this region in Oligocene and Miocene times.

ON THE MOLLUSCAN FAUNA OF THE PATAGONIAN  
TERTIARY.

BY H. VON IHERING.

(Plate XIX.)

(Read April 3, 1902.)

During the last ten years the exploration of the Patagonian and Argentine Tertiary has been very actively prosecuted, but the results of the new studies have not always represented genuine progress.

This refers particularly to the deposits of Entre Rios, which Alessandri regarded as Eocene from his studies of Selachian teeth, while A. Smith Woodward, reëxamining the same material, came to the conclusion that this formation is Miocene or Pliocene. The study of the Mollusca of the Entre Rios beds led me to the opinion that they are Miocene, while Borchert, in view of the large proportion of recent species in this fauna, refers the formation to the Pliocene.

Having at my disposal one of the best collections of marine shells from the Brazilian and Argentinian coasts, I have carefully examined Borchert's work. This author has had access to a much richer collection of Entre Rios mollusks than I myself, in which are represented well-preserved examples of some species—*e. g.*, *Cardium magnum* Born—of which I have seen only casts. This circumstance does not, however, entirely explain the divergence of our opinions, which is rather due to a number of incorrect determinations by Borchert. The small shell which he believes to be *Dione purpurata* Lam. is not referable to that species. The opinion that the young shell differs in outline from that of the adult is refuted by the large series of specimens in my collection. It is not reasonable to attach much importance to such young shells, especially if represented only by a single specimen.

"*Cryptogramma brasiliانا* Gm." is not this species at all, but a different and extinct species, characterized by its numerous coarse concentric ribs, as also by numerous radiating striæ. Beside these two species, the following are certainly erroneously determined:

*Lithodomus patagonicus* d'Orb.*Solecortus platensis* d'Orb.*Modiola tulipa* Lam.*Marginella prunum* Gm.*Nucula puelchana* d'Orb.*Columbella acuta* Stearns.*Tivela argentina* Sowb.

Of the nineteen species which the author regards as still existing at least nine are incorrectly determined. Admitting that the remaining ten species are accurately determined, the proportion of living species in the Paraná formation is as 10 : 60, or 17 per cent.

Borchert's attempt to prove that the Paraná formation is Pliocene must be regarded as a failure; it is opposed to the opinion of d'Orbigny, Philippi and von Ihering, all of whom were well acquainted with South American marine Mollusca, both recent and fossil. *We must continue to regard the Paraná formation as Miocene, while the Pliocene of Argentina is represented in the south by the Cape Fairweather beds, and in the north by the Tehuelche formation.* Of the latter the new collection of Carlos Ameghino contains an instructive representation, with many new species of *Pectinidæ*, *Carditidæ* and *Veneridæ*.

From the marine deposits in the upper part of the *Pampean formation* I have a relatively large collection. As the species are all still living, I am obliged at present to consider the "Pampeano superior" of Ameghino as *Pleistocene*. It is interesting to observe that in this formation are two different horizons, the older of which contains *Ostrea arborea* Ch., *Purpura hamastoma* L., and other species now common on the Brazilian coast, but which are wanting in the later horizon, where they are replaced by *Ostrea puelchana* d'Orb. and other Patagonian species.

With regard to the *Patagonian formation*, many new forms are contained in a large collection sent to me this year by Dr. Florentino Ameghino, and gathered by his brother Carlos in the years 1899 and 1900. This great collection contains representatives of three different faunas, but the greater part of it comes from the Patagonian formation. As I have studied many important collections from this formation, and as my friend Dr. A. E. Ortmann has also discovered many new forms in the collections of the Princeton Expedition, it was very surprising to find a great number of new and interesting forms in this new collection. I reserve the description of these new species until Dr. Ortmann's report has been published, and describe here only two of the most striking new species.

## NAUTILUS CAROLI-AMEGHINOI, sp. nov.

(Plate XIX, Figs. 1, 2.)

*Nautilus testa suborbiculari, imperforata, lævi, suturis simplicibus, siphone interno, in fundo fossæ latæ situ.*

The shell, which is filled with matrix and not very well preserved, is of suborbicular shape, subcompressed and much enlarged toward the aperture. The outer or peripheral part of the shell is rounded, smooth and with simple sutures. There is no umbilicus, but a pit at the central point of origin of the outer lip of the body-chamber. In this groove, the wall of which covers the umbilicus, there is, opposite to the origin of the outer lip, a crista, the prolongation of which passes into the dorsal wall of the body-chamber. The siphon is placed at the bottom of a large and deep hollow, which has an internal situation—that is to say, nearer to the dorsal than to the ventral or external margin of the septum.

*Measurements.*

Major diameter .....	74 mm.
Minor " .....	58 "
Body-chamber, length.....	42 "
" " breadth, central .....	34 "
" " " in the middle .....	29 "

I take great pleasure in dedicating this new species, which is the first representative of the class Cephalopoda from the Tertiary of Patagonia, to Mr. Carlos Ameghino, whose excellent work in the geological exploration of Patagonia I appreciate very highly.

*Locality:* Golfo de San Jorge, Cabo Tres Puntas.

*Formation:* "Patagonico medio."

## NEOINOCERAMUS AMEGHINOI, gen. et sp. nov.

(Plate XIX, Figs. 3, 4.)

*Testa solida, compressa, oblique-ovata, antice posticeque paullulum hiant, concentrice laminato-costata, laminis altis subreflexis distantibus, interstitiis lævibus; auriculis anticis magnis, posticis minoribus; area ligamentale lata brevi.*

The shell is large, solid, very obliquely ovate, slightly compressed and gaping on both sides. The anterior lateral margin is convex, passing gradually into the arched ventral margin; the posterior

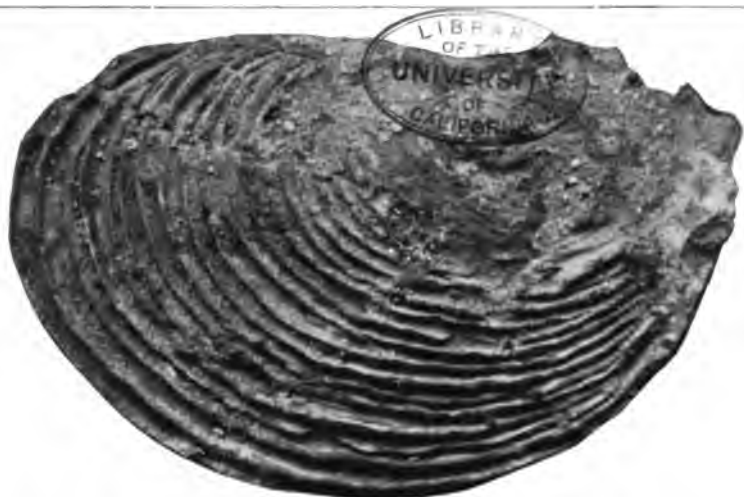


Fig. 3.



Fig. 1.



Fig. 2.



Fig. 4.





margin is concave below the posterior auricle, then becoming convex, passes gradually into the arched ventral margin; the ventral extremity is obliquely produced and convex. The outer surface is provided with numerous concentric ribs, which are three to four millimetres high and slightly reflected along the free margin; the number of these lamellæ amounts to eighteen in the ventral half of the shell; the upper or dorsal half is somewhat defective in the central part. The distance between the ribs is, in general, equal to their height, but there is some irregularity in their size and spacing. Between the ribs the surface of the shell is smooth.

The ligamental area, which is thirty millimetres in length, is destroyed in the central part, as is also the umbo, the situation of which must have been nearly central. The posterior auricle is small, but well developed; the anterior is broken away, but must have been much larger than the posterior. The lateral remnants of the ligamental area are strong, eight millimetres broad and obliquely striated by narrow grooves, separated by small ribs, which are the *direct continuation* of the ribs of the outer surface. It is a remarkable fact that the concentric ribs of the outer surface do not converge toward the umbo, but toward the dorsal margin of the ligamentous area. The inside of the shell shows the simple pallial line, which is distant seven millimetres from the anterior lateral margin and twenty millimetres from the ventral margin. Behind the posterior auricle the shell slopes abruptly toward the margin, while at the anterior margin the transition is gradual. It is impossible to recognize the muscular impressions.

#### *Measurements.*

Length, from anterior auricle to posterior ventral extremity .....	95 mm.
Breadth .....	60 "
Diameter of half-shell .....	22 "

Another specimen, represented only by the ventral extremity, must have had a length of at least 150 millimetres.

*Locality:* Golfo de San Jorge, east of Punta Nova.

*Formation:* Lower part of the Patagonian.

It is not easy to define the systematic position of this species, because the umbo and the central part of the ligamentous area are wanting. The multivincular ligament, the oblique-ovate shape and

the concentric ribs indicate a relationship to the genus *Inoceramus*, from which however it is distinguished by the short and broad ligamental area and the well-developed auricles of the dorsal margin. I regard the species therefore as the representative of a new genus, of which I offer the following diagnosis.

NEOINOCERAMUS, gen. nov.

Genus Aviculidarum testa æquivalvi, oblique-ovata, biauriculata, concentric costata, cardine recto, crasso brevi oblique-sulcato.

I believe this genus to be nearly allied to *Inoceramus*, the species of which are exclusively Mesozoic. Although, because of the incomplete preservation of the specimen described, the systematic position of the genus is not definitely fixed, there can be no doubt that this species represents one of the most remarkable discoveries of Mr. Carlos Ameghino's later expeditions.

I have much pleasure in dedicating this exceedingly interesting species to my friend Dr. Florentino Ameghino, not only in appreciation of his excellent palæontological work, but also as an acknowledgment of the liberality with which he has confided to me the study of the invertebrates of his collection, permitting the types to remain in the Museu Paulista, which for this reason possesses the finest existing collection of Patagonian invertebrates. Of these two new species, one is the first representative of the Cephalopoda from the Tertiary of Patagonia, the other is a new type of Pelecypoda, nearly allied to the Mesozoic genus *Inoceramus*. The collection is also rich in Corals and Echinoderms; among the latter, the study of which I have entrusted to Mr. Lorient le Fort, are also Crinoidea.

With reference to the paper of Mr. Hatcher, I have examined the question of the significance of the Patagonian and Suprapatagonian beds, which Mr. Hatcher regards as only different facies of a single formation. The fact that some species are common to both horizons and that the number of such common species increases with the progress of investigation, induced me for a time to agree with Mr. Hatcher's opinion. It was therefore of importance for me to reëxamine the question with reference to the new material, which was not derived from Santa Cruz, but from northern Patagonia. The result was not favorable to Mr. Hatcher's views. This may be seen from my paper on "The History of the Argentine

Oysters," which will soon be published in the *Comunicaciones del Museo Nacional de Buenos Aires*. Like the species of *Ostrea*, those of *Struthiolaria* are also characteristic fossils of the Patagonian and Suprapatagonian beds, which represent two different sections in one great formation.

Of great interest in this new collection are the fossils from the *Pyrotherium* beds, collected on the Rio Chico, a tributary of the Rio Chubut, and the Golfo San Jorge. Among the mollusks are characteristic *Gryphæa concors* Ih., and *G. pyrotheriorum* Ih., and *Ostrea ameghinoi*. Of species characteristic of the Patagonian formation only two occur: *Cardita patagonica* Sow. var., and *Rhynchonella plicigera* Ih. Among the new species may be mentioned *Bouchardia patagonica*, *Turritella malaspina*, *Struthiolaria striatissima* and *Rostellaria cossmanni*. The last-named species is a representative of a genus which does not occur in the other Patagonian Tertiary formations. In this collection there are neither existing nor Mesozoic species, and I therefore believe the *Pyrotherium* beds to be Eocene, while Florentino Ameghino regards them as Cretaceous.

The general results given in my paper in the *Revista do Museu Paulista*, Vol. II (abstract in English, p. 372 ff.), have not been essentially changed, either by my later investigations or by those of Dr. Ortmann. It is therefore singular that Mr. Pfeffer has, in the past year, repeated his erroneous theory as to the existence of a uniform Eocene marine fauna. Even if we leave out of account the Eocene formations of Patagonia, Chile and New Zealand, we must consider such elementary faunistic facts as the distribution of the Nummulites, which in the northern hemisphere extend from North America to Europe and Asia as far as the Sunda Islands, while they are wanting in the southern hemisphere. These facts cannot be explained by supposed differences of temperature, but only by geographical modifications, for the study of which a knowledge of the Tertiary Mollusca offers one of the most important means.

SÃO PAULO, BRAZIL, October 28, 1901.

## SPECTRA OF GASES AT HIGH TEMPERATURES.

BY PROF. JOHN TROWBRIDGE, OF CAMBRIDGE, MASS.

*(Read April 4, 1902.)*

It seems to me highly appropriate that I should speak in Philadelphia, the home of Benjamin Franklin, on my researches in electricity, and that I should bring to the attention of scientific men here for the first time some remarkable results in the science in which Franklin was a pioneer.

In the Jefferson Physical Laboratory of Harvard University there is a Franklin electrical machine, which was ordered for the College by Franklin when he was one of the Commissioners in Paris. One can with great labor produce by means of it a thin spark perhaps one inch in length. In the same laboratory I have a storage battery of twenty thousand cells which, with suitable transformers, will generate a spark six and one-half feet in length, at a voltage of over six million.

In this practical age, especially in America, one is immediately asked, "What is the use of this great spark?" Probably a similar question was asked Franklin in regard to his smaller manifestations of electricity, and I shall ask you to reflect upon the developments of electricity since his time—the telegraph, the telephone, the lighting of cities, the trolley, the X-rays—and answer for me. You will remember, too, that Franklin, fearing ridicule, which we can charitably think generally arises from lack of imagination, tried his kite experiment in secret. I have not hesitated to build the largest electrical plant at present in existence for the scientific study of electricity, feeling sure that I could reach an unexplored field; and I hope that some of my results which I shall communicate to you will be considered of scientific importance, and will show that I have reached such a field. In the first place, Franklin would see in a spark six feet in length a veritable flash of lightning, brought out of the skies into a laboratory where it can be studied at all times and under almost any imposed conditions. I have discovered that these long sparks do not encounter, so to speak, any greater resistance in passing through the air than sparks one inch in length. The entire current used in propelling the electric cars in this city can pass along the path opened by these long sparks without suffering hardly an appreciable diminution. A rarified hole seems to be

bored, so to speak, in the air, through which, by means of water vapor, what we call electricity passes with a loud explosion. I wish to emphasize this fact in speaking of the scientific results which I have reached with this large electrical plant. I believe that I have proved that water vapor is essential for the passage of electricity through the air or gases. Just as a certain degree of moisture is necessary for chemical reactions, so is water vapor essential for the discharge of electricity through gases. I believe that we have never been able to obtain a perfectly dry gas; and if we should succeed in the future, such a gas would be a perfect electrical insulator.

Since the time of Franklin, the subject of spectrum analysis has been developed. He could study electricity only by means of his eyes. With the spectroscope, however, we now see instead of a blinding flash of white light, lights of many colors—in other words, a spectrum extending from red light to violet light, traversed by many bright lines which are due to the vibrations of the molecules of the components of the air. These molecules are invisible to us until revealed by electricity. The large storage battery I have had constructed enables us to explore a new field in electrochemistry, revealed by the motions of the smallest particles of matter in the world; particles which are everywhere about us, but are only evident when agitated by a discharge of electricity. I can surely claim to have subjected gases to the highest temperature that has been hitherto reached with this interesting result, that the spectra of oxygen, hydrogen, nitrogen, the main components of the air, contain the same spectrum, which is that of water vapor. By modification of the strength of the discharges, one can pass from the blue spectrum of argon to the red spectrum of this gas, which was discovered by Lord Rayleigh, even in tubes filled with hydrogen. This result is accomplished by a powerful dissociation of the small amount of air which is always present in glass tubes, even when great care is taken in preparing the hydrogen. I have obtained many such singular dissociations in hydrogen tubes which have been unsuspected.

Another important fact has been revealed by the passage of powerful discharges through glass tubes filled with rarified gases. I have discovered a rate of molecular vibration to which the photographic plate is apparently inactive. All gases give bright lines in their spectra, and consequently these bright lines are dark lines on the photographic negative. I have discovered dark lines in the

spectra of gases which give, therefore, bright lines on the negative; that is, they do not change the silver salt. This discovery, I think, is of great importance, for it shows that there are rates of vibration to which the photographic plate does not respond. It is imperfect in science as well as in art, and does not give a complete history of the stars, the temperatures of which are probably much higher even than those which I have reached. These dark lines are not due to what is called solarization or to absorption. The solar spectrum is thus probably far more complex even than we have supposed. This new field of what may be called destructive dissociation of gases in which I am working, promises to lead to many important results in the new science of electrochemistry.

[Prof. Trowbridge projected some lantern slides of the spectra of gases obtained with the discharges from the large storage battery, which showed the universal spectrum of water vapor and the remarkable dark lines of which he had spoken.—THE SECRETARIES.]

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## THE INFLUENCE OF ALCOHOLIC INTOXICATION UPON CERTAIN FACTORS CONCERNED IN THE PHENOMENA OF HÆMOLYSIS AND BACTERIOLYSIS.

A PRELIMINARY NOTE.

BY A. C. ABBOTT AND D. H. BERGEY.

(FROM THE LABORATORY OF HYGIENE, UNIVERSITY OF PENNSYLVANIA.)

(Read April 5, 1902.)

In 1896 one of us (A. C. A.) published the results of an investigation upon the influence of alcoholic intoxication on resistance to infection.<sup>1</sup> In that paper attention was directed to the fact that the susceptibility of rabbits to certain types of infection was markedly increased through the influence of prolonged alcoholic intoxication. These results have been fully confirmed by others.<sup>2</sup>

At the time the results were published no fully satisfactory explanation of the mechanism of this phenomenon was available, though several suggestions were offered, viz., the reduced resistance may be referable to the local action of the alcohol upon the gastric mu-

<sup>1</sup> See *Journal of Exp. Med.*, 1896, Vol. i.

<sup>2</sup> See Laitinen, *Acta Societatis Scientiarum Fennica*, Tom. xxix, No. 7, 1900; also *Zeit. f. Hyg. u. Infektionskrankheiten*, 1900, Band 34, S. 206.

cous membrane, thereby impairing the nutrition of the animal to such an extent as to create conditions analogous to starvation, a state in which susceptibility is also seen to be increased; or, to a diminution in the alkalinity of the blood through the acids resulting from the oxidation of the alcohol—such reduction in alkalinity, though slight, has since been shown by Laitinen to occur; or, to the remote action of the alcohol on the nervous system. The value of neither of these hypotheses was, however, susceptible of ready determination, so that the matter rested there for a time.

During the past three or four years a series of brilliant investigations, especially by Bordet, Buchner, Metschnikoff, Ehrlich and Morgenroth and their associates, upon certain physiological phenomena peculiar to the blood and other fluids of the body, have acquainted us with many hitherto obscure and unknown phases of the subject. One of these newly discovered blood reactions seemed especially adapted to the solution, in part at least, of our problem.

It has been demonstrated by the investigators named that an animal may be rendered immune from the intoxicating effects of the blood of another species; that when such immunity is established the blood serum of the immune animal rapidly and completely dissolves the erythrocytes of the alien blood, even when mixed with them in a test tube (hæmolysis); that if such immune serum be heated for thirty minutes to 55°–56° C. it loses its hæmolytic power; and that the power of hæmolysis is at once restored to the heated serum by the addition of a few drops of serum from a normal mammal. These reactions are believed to occur through the agency of two bodies present in the serum—the one a body resistant to low degrees of heat, a “receptor” or “intermediary” body;<sup>1</sup> the other a complementary something, perhaps a ferment, common to all mammalian serums, that is destroyed by heat. The “receptor” or “intermediary body” is conceived to have the property of fixing the invading cells (in this case the blood cells of another species) on the one hand, and the complementary, ferment-like body on the other, bringing and holding them together in a way most favorable to the destructive action of the ferment upon the invading cell. The destruction of bacteria by the fluids of the body is thought to take place in an analogous manner, it being assumed that in the blood are “receptors” having the property of

<sup>1</sup> *Synonyms*—Anticörps hémolytique, Substance preventive, Immune Körper, Amboceptor, Philocytase, Desmon, Copula, Substance sensibilisatrice, Fixateur.



fixing, on the one hand, bacteria, and on the other a "complement" having the power to destroy such bacteria, the relation of receptor to bacteria and to complement being in both cases specific.

The question under consideration by us was:

"Will the sera of animals under the influence of alcohol for varying lengths of time, but otherwise normal, restore to a heated immune serum its hæmolytic activity in the same way as is done by the normal sera of non-alcoholized animals?"

If it will, then the action of alcohol upon the animal organism is plainly not evidenced through a reduction in the amount of the complementary substance so necessary to normal resistance and to immunity. If it will not, then the reverse must be the case.

Should the serum of animals under the influence of alcohol prove to be poorer in hæmolytic "complement" than that of animals not so treated, then there is some justification for the belief that the reduction of resistance to bacterial infections, noted in our work of 1896, may be due to the suppression (in part or in whole) of a "complementary" "proteolytic ferment" (?) that constitutes one of the natural defenses of the body against the invasion of infective bacteria. Without discussing our results in detail, it suffices to say that we found in a number of animals daily intoxicated for a period of about three weeks, the amount of "complement" in their sera to be from fifteen to twenty-five per cent. less than that of normal sera, as determined by the power to "reactivate" a heated immune serum—*i. e.*, to restore to it its hæmolytic properties, a result that we regard as of fundamental importance in explaining (in part at least) the results of investigations made in 1896.

In the course of this work a number of important collateral questions arose, the most significant of which being as to whether the effect noted by us could be interpreted as a general reduction of all complementary substances<sup>1</sup> in the blood, or as only a reduction of a single complement specifically concerned in the phenomenon of hæmolysis; but as their solution is as yet only in the initial stages, it is scarcely necessary to introduce them at this time.

<sup>1</sup> It is believed by Ehrlich and Morgenroth and their associates that the blood contains a multiplicity of complementary elements, each one of which is specifically related to particular receptors and to particular irritants and intoxicants; while Buchner, Bordet, Metschnikoff and their adherents contend that the complement, designated by Buchner and Bordet as "alexine" and by Metschnikoff as "cytase," is a single substance possessed of heterogeneous affinities.

## A BRIEF ACCOUNT OF THE DISEASE KNOWN AS OSTEITIS DEFORMANS.

BY PROF. J. C. WILSON, M.D.

(Read April 5, 1902.)

It will, I trust, be acceptable to the Society if I communicate some facts in regard to a rare disease of the bones.

This affection was first described by Sir James Paget, in the *Transactions of the Royal Medical and Chirurgical Society of London*, in 1877, under the title "A Form of Chronic Inflammation of Bones—Osteitis Deformans." To the five cases which formed the basis of that communication, Paget was able to add in 1890 eighteen further instances of the disease which he had studied. Other cases have been observed in Great Britain; in America up to the present time eleven cases have been reported; a number in France, and a few elsewhere on the Continent of Europe.

It is, however, probable that osteitis deformans is much more common than the number of the published cases would indicate. In the preliminary program of the Association of American Physicians just issued two new cases are announced. The fact that the disease remained long undescribed and is now so seldom recognized, is due not so much to the infrequency of its occurrence as to the trifling subjective symptoms which attend it or their complete absence, its insidious development and slow progress, and the immunity of the bones of the hands and feet. The sufferer from osteitis deformans may develop advanced changes in the skeleton before the deformities attract his attention or that of his friends.

The deformities in some instances affect only a limited number of the bones, more commonly most of them. In the fully developed disease they are usually symmetrical to a remarkable degree.

They consist in the following changes in the skeleton:

Thickening of the bones of the skull and an alteration in its shape. The calvarium becomes flattened, the brow broad, the parietal regions prominent. The general circumference is increased so that the patient has to wear a larger cap than formerly. The bones of the face remain unchanged, so that the facies assume a triangular outline, the base being at the brow, the apex at the chin.

The spine becomes stiffened and curved. There is marked cervico-dorsal kyphosis, with compensating lordosis of the lower

dorsal and lumbar spine. In consequence of this change in the spinal column the head is carried forward and lower than normal, and the height of the patient is reduced—a reduction much increased by the curvature of the bones of the lower extremities and amounting in some of the cases to six or seven inches.

The clavicles are prominent and thickened, the chest short and narrow, the abdomen short and broad and the pelvis wide and low.

Associated with these changes are marked deformities of the long bones of the extremities. The humerus is thickened and enlarged; its surface is irregular, and the shaft is markedly curved, the concavity presenting toward the flexor surface. The ulna and radius show similar deformities and are strongly bent and twisted. The bones of the lower extremities are deformed and bent in a like manner. The femur, tibia and fibula are bent outward and forward.

In fully developed cases the patients bear a curious resemblance to each other. The diminution in stature causes the arms to appear disproportionately long—like those of the anthropoid apes.

The disease usually makes its appearance in middle life and is mostly unattended by subjective symptoms, although in some cases rheumatoid pains have been present at the outset. It has no constant relation to any particular visceral or nervous pathological process, nor to malignant disease as was at one time thought. I have called attention to the high grade of muscular atrophy present in well developed cases.

Paget, whose name has been given to the disease and whose original description remains the best that has thus far appeared, regarded the changes in the bones as inflammatory, and Butlin's account of the histological changes lends support to this opinion.

The process consists of a progressive absorption of bone tissue which becomes porous and rarified; the coincident formation of new bone, which remains for a time uncalcified so that abnormal curvatures develop, and finally dense calcification of the subperiosteal layers of the overgrown and deformed bones. The marrow undergoes fibrous changes. The pathological changes have been especially studied by Butlin, von Recklinghausen, Stilling and Packard Steele and Kirkbride.

The etiology of the disease is involved in complete obscurity. To state that it is due to trophic derangements is a mere general restatement of the facts.

The hypertrophic changes in the bones of an extremity, which

have been shown by Schiff, Vulpian and Philipeaux to follow the section of the nerve supply, cannot be regarded as an analogous process and are not invariable.

Two views suggest themselves: Osteitis deformans may be due to

1. Infection by some organism, to the action of which bone tissue is especially liable; or,
2. To the default of some physiological principle which normally regulates and limits the growth of bone.

Either of these views may serve as a working hypothesis for investigations into the cause of the disease.

This affection has points of similarity with osteomalacia, leontiasis ossea, acromegaly, gigantism, arthritis deformans and rickets, but differs from them all in essential particulars.

No treatment has been of any service in arresting the progress of the disease.

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## IS SCIENTIFIC NATURALISM FATALISM?

A ONE-MINUTE PAPER.

BY WILLIAM KEITH BROOKS.

(*Read April 4, 1902.*)

Berkeley pointed out long ago that all the phenomena in nature may be expressed in terms of motion. The progress of science is teaching us this truth, and is thus bringing us to a point of view which Hume has indicated in these words: "The necessity of any action, either of body or of mind, is not in the object which exhibits the action, but in the spectator."

Scientific predictions are based upon our well-founded confidence that the order which we have discovered in nature in the past will continue in the future; but physical analysis neither answers nor asks why nature should be orderly, or what has made it so. For its purposes, the notions of agency and efficiency and causation are irrelevant and useless, because the notion of necessity is something that we ourselves project into nature and not anything that we find in nature.

If we agree with Hume, as I think we must, does not his statement carry with it, as its complement and counterpart, a declaration to this effect: Freedom in willing and doing, if there be such

freedom, is not in the spectator who considers the action, but in the agent?

Is our failure to find proof of freedom in our bodily machinery and its activity anything more than we should look for if freedom is not in the spectator, so far forth as he is merely a spectator and not a participant?

If the certainty of scientific predictions does not imply necessity, and if freedom in willing and doing is not in the spectator, are we not led to agree with Berkeley, that "certain and necessary are very different, there being nothing in the former notion which implies constraint, and which may not consist with a man's being accountable for his actions"?

If physical necessity is not in nature, but in the spectator; if freedom is not in the spectator, but in the agent; if the certainty of scientific predictions does not imply constraint;—does not the controversy about necessity and freedom come to an end for the man of science? Does science afford any ground for controversy?

## A CLASSIFICATION OF ECONOMIES.

BY PROF. LINDLEY M. KEASBEY.

(Read April 5, 1902.)

Economics has to do with the weal relation between life and the environment. From life, on the one hand, emanates demand for well-being; from the environment, on the other hand, is derived the supply of useful things or goods that minister to well-being. In the last instance, therefore, the weal relation between life and the environment is a relation between demand and supply. Now, demand and supply are connected—made to meet, as economists say—by the utilization of natural resources. The object of this process is to derive from the outer world the qualities requisite to fulfill the demands of well-being, or, more precisely, to convert the potential utilities inherent in the environment into actual utilities. Thus, in its simplest sense, an economy may be defined as a system of activities whereby the potential utilities inherent in the environment are through utilization converted into actual utilities.

The very existence of life implies some such system of activities;

wherever the essential weal relation is established between life and the environment, there the process of utilization is operative. In its widest extension, therefore, the term economy can be applied over the whole range of evolution, from the lowest to the highest orders of animate existence. Furthermore, cursory comparison shows that with the development of life the process of utilization becomes more and more complicated. Thus, regarded from the utilitarian point of view, evolution exhibits a succession of economies increasing in complexity.

It is out of the question, of course, to elaborate this long series in detail. As a matter of fact, no hard and fast distinctions can be established between the several orders of economies, since in each instance the more complex proceed, as it were, by insensible steps out of the simpler, leaving no appreciable spaces between through which lines of demarcation may be drawn. Nevertheless, if we confine ourselves to generalities and content ourselves with obvious distinctions, it is possible to establish the general order of economic development and characterize the several types of economies.

For convenience' sake biologists still distinguish between plant life, animal life and human life, what though they are well aware that the laws of organic evolution to which the three orders of life are subjected are essentially the same. It is possible to establish a corresponding series in the order of economic development, but we must not lose sight of the fact that the differences to be noted are merely differences of degree and in no sense distinctions in kind. This, then, is the primary purpose of the present paper: to indicate the types of economies characteristic of plant life, animal life and human life respectively. It will be seen, when this series is established, that the human economy differs far more from the economies of the lower orders of life, than the economies of plant and animal life differ from each other. Though evidently an elaboration of the preceding types, the human economy is in certain respects so different as practically to constitute a separate system. Having shown this to be the case, I shall devote the remaining portion of my paper to establishing the human economy upon its higher plane.

In the first place, in order to establish the required series of economies, it is necessary to adopt a canon of distinction. To this end I would suggest that characteristic types of economies can be distinguished from each other in two ways: subjectively, according

to the incentive leading to utilization ; and, objectively, according to the means employed in the process.

Applying this canon of distinction in the first place to the simpler systems of activities, it is possible to establish two types of economies—the AUTOMATIC and the INSTINCTIVE—characteristic respectively of the plant and animal worlds.

Under the automatic system the stimulus inciting utilization is involuntary, and as this is the case, the means employed in the process are necessarily natural organs that act without the intervention of the will. Thus plants, for example, as well as some of the lower orders of animals, assimilate the life-sustaining elements inherent in their immediate environment by simple reflex action, involving no conscious effort on their part.

Under the instinctive system, on the other hand, the impulse leading to utilization is voluntary, and as this is the case, the means employed in the process consist for the most part of natural organs that act in obedience to the will. Thus, as opposed to plants, animals may be said to be urged by their appetites to utilize natural resources. It is instinct in their case that induces economic activity. That is to say, the higher animals as a rule are impelled by their natural desires of self and kind preservation to acquire such products of their local environment as go to gratify their own appetites and provide for the preservation of their progeny. And as nature has provided them for the most part with the natural organs necessary to gratify their desires, little or no ingenuity is necessary to this end.

The most complicated economy is that characteristic of human life. In contradistinction to the foregoing, this highly complex system may be designated as the RATIONAL ECONOMY. Right early in the course of their development, human beings appear to have become imbued with an intelligent purpose to meliorate their material condition and so raise the standard of life of themselves and their associates. And not being physically equipped by nature to realize their economic ideals, far back in the course of their career they began to exercise ingenuity in the manufacture of artificial instruments of utilization. Thus, to distinguish the human economy from that characteristic of the animal orders, it may be said: under the rational system the motive making for utilization is purposive, and the means employed in the process consist for the most part of artificial implements manufactured for the purpose.

Having applied our canon of distinction over the whole range of economic development, there appear to be three fundamental types of economies, the automatic, the instinctive and the rational, characteristic respectively of plant, animal and human life. In the automatic economy the stimulus exciting utilization is spontaneous, and the means employed in the process consist of natural organs that act without the intervention of the will. In the instinctive economy the impulse leading to utilization is voluntary, and the means employed in the process consist for the most part of natural organs that act in obedience to the will. In the rational economy the motive making for utilization is purposive, and the means employed in the process consist for the most part of artificial implements manufactured for the purpose.

The foregoing classification gives a general idea of the order of economic development, and enables us to distinguish superficially between the three fundamental types of economies. The distinction between the automatic and the instinctive systems, it will be noticed, is not nearly so marked as that between these simpler systems, on the one hand, and the highly complex human economy on the other. Indeed, if Professor Loeb is right in regarding instinctive action as essentially the same as reflex action, the separation of the instinctive economy from the automatic economy must be taken to express simply a superficial distinction, or at most to mark a minor difference of degree. Rational activities are, however, radically different from instinctive acts, though here too, no doubt, the difference is ultimately one of degree. Wherein these latter differences consist is the task of the psychologist to show. It is enough for the economist to take cognizance of the facts and establish his distinctions accordingly. On the face of it, the fact that the human economy constitutes a rational system evidently places it upon a higher plane than the economies characteristic of the lower orders of life. Then, again, regarded from the point of view of economic development, a further distinction is discernible in the process of utilization characteristic of the rational system. In the rational economy utilization appears to make for progress; whereas under the automatic and instinctive systems utilization seems to be simply conservative.

It is evident enough, as has already been indicated, that with the development of plant and animal life the process of utilization becomes more and more complicated, but in all these cases increased complexity appears to be rather the effect of variation and selection



than the outcome of economic initiative. Thus the instinctive system, characteristic of the animal world, becomes more and more complicated as we advance from the lower to the higher orders of animal life; but there is nothing to indicate that this increase of complexity is due to conscious effort on the animal's part. Lamarck, it is true, attributed appetency to animals and endeavored to prove that evolution is to a large extent the result of active initiative; but modern opinion still inclines to the belief expressed by Darwin that the process is effected unconsciously, through natural selection. But it is not necessary at this juncture to go into this abstruse question of the relative importance of appetency and variability in the evolutionary process. We are dealing, it will be remembered, merely with differences of degree, and may accordingly content ourselves with establishing obvious distinctions. This much at least is evident from casual observation: if we exclude the development of the human species from our survey, progress in the economic sense is not a notion that can properly be applied to the evolution of animal life, and of course much less to plants. Even the highest animals, when once adapted to their environment, show no disposition in their natural state to improve their material condition or meliorate the lot of their progeny. On the contrary, to the extent that they remain uninfluenced by selection, animals and their offspring appear to be urged by the same appetites, to utilize the same resources in the same way from generation to generation. The impulse leading to utilization is in their case instinctive, and therefore more or less rigidly determined along certain definite lines. And inasmuch as nature has provided them with the means of utilization, it is not necessary for them to exercise ingenuity in the invention of artificial instruments. Some animals do, to be sure, manufacture artificial implements of production—witness, for example, beavers that build dams, or certain ants that actually cultivate their fields. Still even in such cases nature supplies the necessary tools, and it would be difficult to find instances in which animals were led to improve their productive processes with a view to meliorating their material condition. Thus, from the fact that the impulse leading to utilization is in their case instinctive, and from the further fact that the means employed in the process are for the most part natural organs that act without the intervention of intelligent foresight on their part, animals may be said to subsist in a circle. Appetite impels them in first instance upon their food quest, and the

nutriment when acquired is assimilated. During the process of digestion a period of rest or play ensues until the original appetites are re-aroused, when hunger again sets them in search of subsistence with the same result. The life of the anaconda is the most striking example of this circular sort of existence, though the description applies in a less degree to all orders of animals, whose existence for the most part amounts to a monotonous round of acquisition and assimilation as long as life lasts, and is afterwards carried on in much the same way by their offspring. Obviously there is nothing in such a system to stimulate progress, for the economic sequence once established is recurrent: demand tends toward utility, utility leads to utilization, and utilization results in supply, over and over again.

Turning from the instinctive to the rational economy, the phenomenon of progress becomes immediately apparent. If we extend our survey to include the activities of mankind, it is evident enough that utilization is a potent factor of development. Not that the human species is not subject, like all other animals, to the process of selection; by no means—indeed, as ethnology shows, the human species has in the course of time, through the interaction of variability and environment and by dint of selection, become differentiated into a number of ethnic stocks. Only the process of human development does not appear to stop there. In man's case—and, as far as I can see, in man's case alone—utilization has made for further progress along economic lines. That is to say: men of the same descent, who do not differ from each other ethnically to any appreciable extent, who are to all intents and purpose alike as far as structure and function are concerned, still exhibit striking differences in their manner of life. Thus the Frenchman of the provinces and the Frenchman of Paris are ethnically alike, but differ enormously in their economic activities. And offspring that vary ever so slightly from their parents in the organic sense very often show decided increase of economic capacity. For example, the Englishmen of to-day are very much like the Englishmen of three hundred years ago, but in their manner of life they differ widely from their ancestors. On the other hand, people of diverse ethnic stocks, if placed under the same economic conditions, soon conform to an established standard of life and adopt similar ways of living. Our own country furnishes a striking instance of this. The population of the United States is recruited from all countries of the world, but

despite this ethnic divergence a distinctly American standard of life has been established to which all citizens, foreigners and natives alike, endeavor to conform. Since such are the facts it is evidently necessary in man's case to draw a sharp distinction between progress through selection and progress by utilization—between what may be called ethnic variations and economic distinctions.

Let us examine the situation a little more closely. Looking first to the subjective side, human beings do not seem to be content, as most animals are, to consume the same goods day after day, year after year, and from generation to generation. On the contrary, man appears to be bent on obtaining variety. The gratification of one set of desires seems to cause a new series to emerge in the mind. We imagine we shall be satisfied with what we want, but acquisition soon convinces us to the contrary—like the boy who found a watchkey, and on the basis of this possession asked his father for a watch. In short, the mere fact of acquisition extends the horizon of our wants and arouses a desire for further acquisition; or, to put it in economic terminology, the possession of certain essential goods stimulates a demand for complementary goods. Without dwelling on this psychic phenomenon, so familiar to us all, it may be stated as a general proposition: human beings naturally seek variety and strive to extend the scope of their consumption.

The emergence of new wants in men's minds naturally suggests a corresponding series of satisfactions; demand is necessarily correlated with supply. Suppose we turn, then, to the objective side and take the extrinsic factors into account. The moment the conditions of supply are considered, it becomes apparent that man's desire to extend the scope of his consumption is met by obstacles arising from the character of the environment. Outer nature affords a few free goods, it is true, but by no means enough to satisfy man's expanding wants. For the rest, raw materials must be transformed into pleasure-giving products by artificial processes. To this end implements are necessary, since human beings are not equipped, as most animals are, with the technical means of production. Organization is also essential, as it is only through the systematic division and association of their productive forces that men are able to provide the requisite variety of goods. Because his expanding wants outstrip his inherited capacity, to overcome the obstacles arising between demand and supply, man is accordingly

required to exercise ingenuity in invention and undertake economy in organization. Or, to express it more concisely: in order to extend the scope of their consumption human beings are compelled to improve their means and methods of production.

Putting two and two together, the situation seems, then, to be this: man's desire for variety urges him to extend the scope of his consumption, and in order to extend the scope of his consumption he is obliged to improve his means and methods of production. Thus, in contradistinction to the circular sort of existence characteristic of animal life, the course of human progress is upward, so to speak, along the lines of a spiral. The emergence of elementary wants in men's minds stimulates invention and organization and results in the production of goods. The consumption of these essential goods causes wants for complementary goods to emerge in the mind, and these new wants in turn stimulate further invention and organization. Thus new wants call continually for the improvement of productive processes, improved productive processes provide a further variety of goods, which in being consumed cause still other wants to emerge in the mind that call for further improvement of productive processes, and so on; want inducing satisfaction and satisfaction inducing want almost indefinitely.

Thus in the rational economy the economic sequence is progressive and not merely recurrent as in the instinctive economy. Instead of demand tending toward utility, utility leading to utilization, and utilization resulting in supply over and over again, as is the case with most animals, in man's case expanding demand tends toward the augmentation of utility, the augmentation of utility leads to increasing utilization and increasing utilization results in the differentiation of supply.

## DRIFT CASKS IN THE ARCTIC OCEAN.

BY HENRY G. BRYANT.

*(Read April 3, 1902.)*

Among the many notable sessions of this venerable Society, perhaps none in recent years have been more interesting than the "Nansen" meeting held on the afternoon of October 29, 1897. It was one of the last occasions on which our late President, Frederick Fraley, occupied the chair. The occasion was noteworthy, not only by reason of the paper on "Some of the Scientific Results of the Fram Expedition," read by the distinguished Norwegian explorer, but also because of the supplementary discussion which gave opportunity for Rear Admiral George W. Melville and other competent authorities to give expression to their views on the importance of Arctic research and the best methods of prosecuting it in the future.

In the course of his discourse on "The Drift of the Jeannette," Admiral Melville—after recommending that future attempts to explore the unknown area should start from the Bering Sea side—called attention to the fact that much valuable data relating to circumpolar currents could be obtained by setting adrift in the waters north of Bering Strait specially constructed casks containing the requisite records. A certain percentage of these floating messengers might fairly be expected to survive the perils of the Arctic pack and eventually be looked for in waters adjacent to Franz Joseph Land, Spitzbergen or Greenland. In this connection he remarked: "I do believe, however, from the information we have gained from the drift of the Jeannette and the Fram, that vessels of any kind, such as casks or driftwood, will come out by way of Spitzbergen—though not necessarily across the Pole. The only reason for sending men in ships is, that they may be observers to make a daily record of events. . . . But for this, I say, a hundred casks, properly numbered, made after the manner of a beer keg of twenty gallons capacity, properly hooped, and the ends extended out to complete a parabolic spindle, would demonstrate the drift."<sup>1</sup>

This idea of studying ocean currents from data obtained from "bottle messages" is not entirely new, and has, in fact, been employed by the Hydrographic Office of the U. S. Navy and by

<sup>1</sup> "The Drift of the Jeannette," *PROC. AM. PHIL. SOC.*, Vol. xxxvi, No. 156.

other agencies for some years past. But in such cases the messages have been enclosed in an ordinary bottle and have been distributed along the ordinary routes of ocean travel. But the idea of investigating circumpolar currents by means of specially constructed drift casks originated, I believe, with Admiral Melville, and the project possesses certain features which will commend it to that large body of students who are interested in the problems of oceanography. On another occasion I outlined some of the preliminaries of this experiment, and in this connection I venture to quote from that statement of the subject:<sup>1</sup>

"This proposed method of studying Arctic currents without endangering human life having been brought to the notice of the Geographical Society of Philadelphia, that body determined to undertake the project. In view of the exigencies of a long voyage on the floe ice, special attention was given in the construction of the casks to shape and strength of materials. Thus, to more readily escape crushing by the ice, as intimated above, their shape conformed to that of a parabolic spindle, while they were made of heavy oak staves one and one-quarter inches thick, encompassed by iron hoops three sixteenths of an inch thick and two inches wide. A coating of black 'half stuff' (pitch and resin mixed) was then applied. In addition to the preservative qualities of this coating, the thickness of the wood and metal used is believed to be sufficient to resist the attrition of the ice and the effects of corrosion during the long drift. The staves, so tapered as to form the spindle, were covered on the ends by light galvanized cast-iron caps, held in place by an iron rod five-eighths of an inch in diameter, extending the length of the cask and secured by conical nuts at each end. As above stated, a heavy coating of black water-proofing material was applied to the casks to guard against corrosion and decay. From the color used they will be more easily seen, and will also the more readily sink—under the action of the summer sun—into the body of the ice and be preserved from destruction by crushing. The number of each cask was etched into the wood, as well as painted on the outside. In accordance with the instructions of the originator of the plan, the vessels must be placed on the heavy floe ice. If set adrift in open water they would be too much at the mercy of winds and waves, whereas by being deposited on heavy ice, which

<sup>1</sup> "Drift Casks to Determine Arctic Currents," by Henry G. Bryant, *Verhandlungen des Siebenten Internationalen Geographen-Kongresses*, Berlin, 1899, Zweiter Theil, Seite 663.

is more affected by under currents, they will probably be carried on a more correct drift. A reinforced bung-hole with bung was provided, and through this the message bottle was inserted. . . . This latter consisted of a narrow cylindrical tube made of flint glass, and technically known as an 'ignition tube,' accompanying which were suitable corks and sealing wax. As an additional precaution, these tubes were in turn enclosed in cases made of maple wood provided with screw tops.

"The message paper enclosed in this way was printed on linoleum paper by a permanent blue-print process, which renders it practically impervious to salt water. The enclosed message was printed in the English, Norwegian, German and French languages, and embodied the following particulars:

"(a) Space for name of vessel and master assisting in distribution, date, number of cask, and latitude and longitude of point where it was set adrift.

"(b) Directions as to filling in record and sealing up tube.

"(c) Blank space for insertion of name of finder, date and locality where cask was picked up.

"(d) Clause requesting finder to forward message paper to the nearest United States Consul at his home port, or to send it direct to the Geographical Society of Philadelphia.

"Accompanying each consignment of casks was a set of printed instructions to masters of vessels engaged in their distribution."

In the important and hazardous work of distributing the fifty casks provided for the experiment, the promoters of the enterprise have received the assistance of the U. S. Revenue Cutter Bear, which makes yearly trips to Point Barrow, Alaska, in the interests of the American whalemén. We have also profited by the coöperation of the Pacific Steam Whaling Co. and of Messrs. Liebes & Co., of San Francisco, both of whose vessels have assisted in placing the casks adrift in the far North. The reports of the accomplishment of this preliminary work have come in rather slowly owing to the length of the whaling voyages and other causes. Thus the first consignment of casks was shipped from San Francisco as early as March, 1899, and the others as soon after as opportunity offered; and yet, of the thirty-five casks whose distribution has thus far been reported, intelligence of the last distribution arrived here no later than December 11 of last year.

Thus only within the last few months has it been possible to report definitely in regard to the launching of the greater number

of the casks, and I have, therefore, availed myself of the present opportunity to present some details relating to the present status of the experiment. The directions to masters of vessels having in charge the distribution embodied the main ideas of the originator of the plan and recommended "that special efforts be made to carry a number of casks north of Bering Strait and thence to the westward, where a number of them should be set adrift at or near Herald Island. Then proceeding northward along the eastern edge of the ice pack until the highest safe latitude is obtained—say lat.  $75^{\circ}$  N., long.  $170^{\circ}$  W. from Greenwich. . . . At this point final sets of casks are to be set adrift to demonstrate, if possible, the currents to the eastward or northward and eastward, if any there prevail." In examining the reports sent in, I find that these instructions have been carried out in a praiseworthy manner. Thus I find, by plotting the positions indicated, that on August 19 and 21, 1901, the U. S. Revenue Cutter Bear, under Capt. Francis Tuttle, placed fifteen casks adrift at three different points on the floe ice north and northeast of Herald Island, making a northing in one instance of  $72^{\circ} 18''$  near the  $175^{\text{th}}$  meridian of west longitude.

In September, 1899, Capt. D. T. Tilton, of the S. S. Alexander, belonging to Messrs. Liebes, placed four casks adrift south and east of Herald Island, and in the same month Capt. Sherman, of the Pacific Steam Whaling Co.'s steamer Thrasher, discharged one cask W. N. W. of Point Barrow, while in September of last year (1901) the same company's vessel, the Narwhal, succeeded in launching three casks in three different locations well north and west of Herald Island. The highest northing yet reported as a delivery of the casks was attained by the vessel just mentioned on September 7, 1901, when  $73^{\circ}$  N. lat. was reached.

Thus we find that twenty-two casks have been successfully launched at different periods on the great ice pack north and northeast of Herald Island.

With a view of testing the probable existence of a northeastern or North American drift through the Parry Archipelago, and along the route followed by McClure fifty years ago in accomplishing the Northwest Passage, the whaling captains were requested to distribute some casks in the region of Banks Land, near the western approach to the Northwest Passage route. This plan coincided with the movements of the whaling fleet, the members of which frequently extend their voyages for considerable distances east of their winter



rendezvous, Herschel Island. Hence we find that some nine casks were set adrift off Banks Land in 1899 and 1900 by the steam whalers Alexander, Thrasher, Narwhal and Beluga. It seems to be altogether reasonable to assume that quite a large percentage of the water contributed to this part of the Arctic Ocean by the Mackenzie River should find its outlet by means of the devious channels which extend eastward among the islands of the American Archipelago; but just which route the drift casks will take, or how long it will take them to reach the whaling grounds in Lancaster Sound, it is idle to conjecture. Should any number of the casks be recovered on the Atlantic side, however, the time occupied by them on the journey between the known termini can be ascertained with some accuracy, and the resulting data should throw some light on the speed of the current in question. From the representatives of this miniature flotilla which were cast adrift in the waters north of Bering Strait, we may look for more definite results.

It has been known for years that no appreciable amount of water from the Polar Ocean escaped through the narrow, shallow outlet of Bering Strait, while the knowledge gained from the drift of the Jeannette and Fram point to the existence of a well-defined drift across the circumpolar area to the shores of Franz Joseph Land, Spitzbergen and East Greenland. The presence of quantities of Siberian driftwood in the localities named can be explained by no other intelligent hypothesis, while it is well known that Dr. Nansen based the theory of his voyage primarily on the finding of the Jeannette relics on the west coast of Greenland, three years after the crushing of that vessel in the sea northeast of the New Siberian Islands. Prince Krapotkin, the distinguished Russian writer, gives due importance to the Jeannette's voyage as bearing on the solution of this problem, and commends Nansen for "embodying the drift of the Jeannette and the East Greenland ice drift in one mighty current. A formidable ice current, almost as mighty and of the same length as the Gulf Stream, a current having the same dominating influence in the life of our globe, has thus been proved to exist."<sup>1</sup> Those who are interested in this experiment indulge in the hope that these casks, which have been consigned to the sea ice near the locality where the Jeannette began her drift, will pursue their voyage across the Polar basin impelled by the same elemental forces which carried the Jeannette so far on her journey,

<sup>1</sup> "Recent Science," *Nineteenth Century*, February, 1897, p. 259.

and which subsequently swept the brave little Fram across a great portion of the unknown area.

From the nature of the case, it is difficult to prophesy the time that will be required to complete the drift.

The Jeannette was put into the ice in latitude  $71^{\circ} 35' N.$  and longitude  $175^{\circ} W.$  and consumed twenty-two months in making her zigzag drift of 1300 miles. The provision list signed by Lieutenant DeLong, and the other articles believed to belong to the Jeannette, were three years in traversing the distance from the place where that vessel was crushed in latitude  $77^{\circ} 15' N.$ , longitude  $155^{\circ} E.$ , to the point where they were picked up by the Eskimo, off Julianhaab, in South Greenland, a distance of 2900 miles.<sup>1</sup>

Assuming that the resultant of the drift of these casks will be the same as that of the Jeannette before she sank, and assuming that their subsequent drift will be at a rate of speed corresponding to that of the relics—that is, about 2.6 miles per day of twenty-four hours—we find that a period of about five years will be required to bring them to the same locality; but it is only fair to assume that a certain percentage of the casks which are carried in this great current—estimated to be 300 miles in width—will find their way to the shores of Franz Joseph Land, Spitzbergen or Nova Zembla, in which event the chances are quite good of their being recovered at an earlier date by Norwegian walrus hunters or fishermen.

The controlling influence of winds in their relation to the recognized and well-defined ocean currents is a fact accepted by all meteorologists at the present day. It is said currents are set in motion by this agency which attain a speed of from three to four miles per hour. If such is the case where the ordinary ocean surfaces are concerned, how much more potent must the impelling force of the winds be in conditions where countless ice surfaces are presented to its action. In reading of the drift of the Jeannette, nothing is more striking than the rapid progress the imprisoned ship made in the summer months as a result of the influence of the continuous southeast winds which prevailed. Admiral Melville alludes to the effect of innumerable hummocks of ice, "like millions of sails set to catch the breeze," and states that after each of these disturbances had subsided a setback drift to the southeast set in.<sup>2</sup> The experiences of the Fram party appear to have been quite similar; and these facts would seem to point to some uniform and

<sup>1</sup> *The Farthest North*, Dr. Fridtjof Nansen, Vol. i, p. 19.

<sup>2</sup> "The Drift of the Jeannette," *Id.*

consistent set of conditions which may be explicable from a meteorological standpoint. The published weather charts show that there is an area of low barometric pressure where a cyclonic disturbance takes place whose centre in summer time is well north of Bering Strait, and which in yielding to seasonal changes drops down at the approach of winter to a region south of Bering Strait.

Thus in the summer months this centre of disturbance would be north of the position occupied by the Jeannette, and winds in following their accepted course from west to east would naturally be drawn in and approach the cyclonic area from the southeast, causing the continuous gales referred to by Admiral Melville.

Meteorologists also refer to the existence of a centre of cyclonic disturbance between the 70th and 80th parallels of north latitude, which, following the general law, progresses with the seasons on a more or less uniform path from west to east around the Polar basin. The presence of this moving centre of attraction (if it is accepted as an existent factor in circumpolar meteorology) must exert a controlling influence on the winds of this region, and it follows as a logical sequence that the direction of the ocean currents must be regulated by the same phenomena. Without claiming any special knowledge of this branch of the subject, it occurs to me that in this connection we may find an explanation of the existence of more or less constant winds at certain times of the year in the region referred to, and in these phenomena may lie the interpretation of the reality and constancy of the great Polar current.

With the generous coöperation of the various agencies mentioned, the drift-cask experiment has been successfully inaugurated. It is our intention to bespeak the aid of the U. S. Consuls in northern Europe likely to come in contact with seafaring people who may visit the northern waters where these casks may eventually put in an appearance. It is hoped that such publicity will be given to the project, that when the time arrives for these inanimate messengers to appear in waters frequented by men, a certain percentage of them may be recovered and reported upon.

We look forward with keen interest to the outcome of the present campaign of the gallant Peary, and to the efforts of the superbly equipped Baldwin-Ziegler expedition in its attack on the Pole.

To the Norwegian expedition under Sverdrup and the Russian one under Baron Toll, we also wish a full measure of success. And we trust all these explorers will return with important contributions to our knowledge of the far North.

Should the prize of the centuries be denied to these intrepid voyagers, however, it may be that some devoted enthusiast will be moved to attempt to explore the unknown area in an expedition planned on the lines of the Fram voyage, which after all promises the greatest chance of success.

In such an event it is hoped that the data secured as a result of this drift-cask experiment may be found to be a contribution of some value to the hydrography of the Arctic regions.

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## BLINDNESS FROM CONGENITAL MALFORMATION OF THE SKULL.

(Plate XX.)

BY CHARLES A. OLIVER, A.M., M.D.

(*Read April 5, 1902.*)

Congenital malformations of the skull assert their evil effects upon the integrity of the tissues of the visual apparatus and its consequent functioning in definite ways. Should the disturbing factors be set into activity during intrauterine existence, while the cranial bones are passing through their primary stages of development, the direct effects of such disturbance will be so great that not only will organic changes appear in the ocular structures, but coarse associated faults will manifest themselves in the related and contiguous tissues.

The posterior portion of the cranium is proportionally the largest during the early stages of development of the skull, the parietal regions beginning to enlarge at about the eighth week of intrauterine life, followed soon afterward by the frontal and the occipital regions.

The newly born cranium is relatively very large in comparison with the rest of the body. In contrast with the facial portion it exhibits a predominance of the cerebral part in proportion of seven to one. The six membranous fontanelles and the fibrous septa between the adjacent osseous structures continue intracranially with the dura mater and extend extracranially to form the pericranium, giving rise to sacs in which bony plates without diploë are situated. At this period of life there are cartilaginous areas scattered through the occipital bone, while the presphenoid portion of the sphenoid

bone fails to exhibit any of the sinuses that are seen in adult life. The optic foramina are large in size and triangular in shape, having been obtained by the confluence of the presphenoidal and orbitosphenoidal centres. The superciliary ridges and frontal sinuses are not yet present. The lacrymal bones consist of simple delicate sheets. As a rule, the nerve foramina occupy sutural points or positions of ossific centres.

Both the primary and the secondary foramina, particularly the latter, are disturbed by distortion-processes taking place during their passage through many complicated bony tunnels before they escape through the dural sheath, as is primarily done by the former types.

Minor arrests and perversions of development in the bones of the upper face are so frequent that they constitute the daily findings of the scientific ophthalmologist and trained optician. Orbital deformities, more especially those of the rim of the orbit, are very common, and although they have decided effects upon refractive error and exterior-ocular muscle-equilibrium, they fail to exert but little, if any, damage upon combined visual functioning when the resultant functional faults are either orthopedically or radically corrected. More pronounced osseous deformation, the result of disturbances of development of the bones of the face, show coarser signs of fault in the eyeballs and their adnexa; exhibiting, for example, monolateral and bilateral stenoses of the nasolachrymal ducts. In the grosser forms of congenital malformation leading to antenatal or, later, postnatal blindness (the subject-matter of this communication), it is probable that the primary changes have taken place in the notochordal and trabecular regions during the chondral stages of development of the brain-case. In these types, both irregular ossification with consequent cranial contraction in one situation and undue expansion in another, and undue sutural closure from inflammation of the osteophytic membranes with resultant thickenings and ridge-like eminences along the osseous junctures, especially in the basilar series of bones at their asteriorial, inional and lambdal points of junction, may appear.

The normal morphology of the skull is expressed in three stages. The brain vesicles are at first enclosed in a thin delicate sac, a part of which gradually hardens into a fibrous membrane, while the rest persists to form the dura mater of postnatal life. The second stage is represented by a partial conversion of the metamorphic tissues into

cartilage, particularly at the sides and the base of the membranous cranium. During the third stage, true osseous material obtained from both the membrane bones and cartilage bones appears, until finally a more or less completed bony covering containing remnants of chondral matter is obtained.

The occipital bone originates from four centres: the basioccipital, formed from cartilage at about the seventieth day; the two exoccipitals, also derived from cartilage a few days later; and the squamoccipital, composed of two parts, the interparietal and the supraoccipital, which appear from separate nuclei at about the eighty-fourth day, and unite in about twenty-four days' time. At birth all of these parts are connected by cartilaginous strips. They are not fully fused until the seventh year of postnatal life, the two exoccipitals and the squamoccipital becoming ankylosed some two years later.

The sphenoid bone arises from twelve bone nuclei arranged in pairs, these being divided into two pair for the presphenoidal and four for the postsphenoidal centres. These centres successively appear from the fifty-fourth to the ninety-first day of intrauterine life.

The parietal bones are of interest, as they constitute a great portion of the vault and sides of the skull, and are in direct relationship with some of the most important sutures—the sagittal with its fellow, the coronal with the frontal, the lambdoidal with the squamoccipital, and the squamus with the squamal; the anterior inferior angle articulating with the sphenoid, and the posterior inferior angle articulating with the mastoid portion of the petrosal. As a rule, each parietal bone ossifies from a single earthy spot, situated in the outer layer of the membranous covering of the cranium, at about the forty-second day of intrauterine existence.

The frontal bone, another important suture-bearing roof bone, arises from two earthy spots in the external layer of the membranous covering of the cranium, about a week later than those that are intended for the parietal bones. These two portions, as a rule, unite soon after birth by a median suture-line known as the metoptic. Ankylosis commences at about the second year of postnatal existence. A portion of the bone helps form a part of the orbits and has its main connections with the ethmoidal, the lacrymal, the malar, the superior maxillary, the nasal, the parietal, and the sphenoidal bones.

The epipteric bones, wedged between portions of the frontal, the parietals, the sphenoid and the temporal bones, are of importance in this study. They are present from the second year of life to about the age of adolescence; they then persist as true ossicles or help to form new sutures. They are variable in size.

The Wormian bones, that at times are found in great numbers in the various sutures of the cranial part of the skull, must also be considered of value in this connection.

The sphenoid bone, the most important and the most irregular of the basilar bones, is situated in the region of the anterior and middle fossa. It practically contains all of the foramina and fissures intended for the emergence and the exit of the sensory and motor nerves, blood vessels and lymph channels connecting the intracranial and external portions of the visual apparatus. The middle fossa is the most complicated of the three great depressions in the floor of the cranial cavity, it containing all of the most important nerve communications and vascular and lymph channels that are in association with the optic nerves and eyeballs. The posterior fossa hold the occipital lobes in their subdivisional cerebral fossa, that are situated above the groove that is intended for the course of the lateral sinus.

It is a well-known fact that cranial asymmetry is almost universal. Study of the main foramina and fissures of the various orbital cavities of man exhibit marked variabilities in their relative sizes, shapes and positions. The average depth of the orbit of the Negro race, for example, is at least an eighth greater than it is in the orbit of the Caucasian; while the early ossification of the septum with the superior maxilla in the same race produces a normal flattening of the glabella, with a lateral broadening of the alæ of the nose. Moreover, in this class of subjects the characteristic prognathism of the race becomes apparent when the individual has passed the pubertal period, at which time of life an over-development of the inferior maxillary bone occurs. Here there is type-form of individual with a flattened nose, a wide interpupillary distance, a broad, flat forehead and a projecting malar prominence, that are all so characteristic of the usual brachycephalic head: here there are individuals representing one of the principal subspecies of human life in whom there are probable retentions of some of the most pronounced features of the quadrumana; a true acceleration, as it were, passing beyond the Caucasian retardation of embryonic development.

It is not, however, with these minor and relatively undisturbing types that this communication deals. It is with the grosser forms of cranial malformation; those that particularly involve the basilar fossa and their many fissures and foramina; types which sooner or later give expression to blindness as one of their most prominent and characteristic symptoms.

The gross configuration of the skull and the condition of the various portions of the visual apparatus are so strictly in accord with one another, that certain forms of cranial asymmetry can, with almost definite precision, be associated with certain kinds of blindness. Five coarse clinical types of cranial deformation—the well-known oxycephalic, the scaphocephalic, the leptcephalic, the trigonocephalic, and what I have elsewhere described as the occipital or occipito-parietal—may be cited.

The oxycephalic or even the gross hypsicephalic type is characterized by the so-called steeple-shaped or dome-like head. It is dependent upon an improper union of the parietal bones with the occipital bone, the temporal bones and the sphenoid bone, producing compensatory over-developments along the sagittal suture and in the position of the anterior fontanelle. The pterion region with its anterior lateral fontanelle and later Wormian bone, and the region of the lambda marking the situation of the posterior fontanelle, with its intervening sutures and angular articulation, are all too early united and ankylosed, giving rise to corresponding relative disturbances in the calvarial portion of the cranium, particularly along the sutural lines and in the most nearly related fontanelles.

In this type, which may be very slight or of the grossest character, as shown in the accompanying reproductions of two undeniable cases occurring in my public practice at the Philadelphia and Wills' Hospitals (Plate XX, Figs. 1 and 2), the visual signs of the disease vary from the veriest eye symptom to the coarsest ocular expression, and may first appear at any time during early or middle life.

CASE I.—The gross example shown in Fig. 1 was that of a sixty-two-year-old negro, who, with a history of an acute attack of convulsive seizures from fright, occasioned, he asserted, by a fall<sup>1</sup> at one year of age, had three years later the expression of "pop-eyed" epithetically applied to him, this pseudonym having since persisted throughout life.

The patient stated, and I one day had a clinical demonstration of the

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<sup>1</sup> The postnatal fall as a causative factor for the cranial malformation must be rejected when the congenital stigmata are considered.



same, that he had more than once pushed his right eye out between the lids. Five years before I saw him he accidentally discovered that he could not see with the left eye. Two and a half years after this the sight of the right eye began to gradually fail, until at the time of examination it was found that vision with it was reduced to a faint doubtful perception of light in an inferior temporal field. The left eye was blind. The superficial areas of the two orbits were immense. The lids were large and the palpebral fissures were broad and long. When the position of the left eye was gauged so as to have its supposed visual axis directed straight ahead, the right eye projected two and a quarter millimeters forward beyond the superior and the inferior margins of the orbit, and diverged some thirty degrees out and three degrees down. When the right eye was placed in the same relative position, the left eye was found to be almost as greatly diverged and was directed somewhat more downward.<sup>1</sup> Curiously, extraocular motion was very little if at all disturbed, although palpation showed that the eyeballs were situated in extremely shallow, almost saucer-like orbits, the shallowest portions of the cavities being situated toward the median line. The corneal epithelium was thickened and the deeper structures of the membrane were opaque in a couple of places. The pupils were large and the irides seemed disproportionately sluggish in their various reactions to the amount of local disturbance. Both lenses presented evidences of dense secondary degeneration, that of the left eye being so opaque that the fundus of the organ was invisible. A faint red glare, with the appearance of a few retinal vessels—best seen with a minus spherical lens of twenty diopters' strength—made it probable that portions of the secondary ocular lesions were due to a high-grade myopia. Intraocular tension in each eye was normal. The anterior scleral vessels were not engorged, and there was not any ciliary tenderness.

The conformation of the skull was typical. The lower jaw, which was increased in size, was mesognathous, if not prognathous in shape. The condition of the hands, as seen crossed upon the body, discredited the belief of any disease of the pituitary body. The bitemporal diameter of the skull was but thirteen and a half centimeters, and the biparietal was but one and a quarter centimeters wider. The occipito-frontal diameter equaled eighteen and a half centimeters, while the occipito-mental was somewhat in excess of twenty-six centimeters. The trachelo-bregmatic diameter was twenty-three and a half centimeters in length.<sup>2</sup>

<sup>1</sup> The exophthalmus and divergence can be easily differentiated by examination of the reproduction of the photograph of the case.

<sup>2</sup> I am under obligations to Dr. Clarence Van Epps, one of my Residents in both institutions, for presentation of the copy of the photograph of the first subject taken by Mr. James F. Wood, of Philadelphia; to Dr. Frederick C. Krause, one of my former assistants, and now Assistant Ophthalmic Surgeon to





FIG. 1.



FIG. 2.



FIG. 3.

BLINDNESS FROM CONGENITAL MALFORMATION OF THE SKULL.—(OLIVER.)

The second example of the type, in a German, an excellent illustration of possibly an extreme hypsicephalic skull with a preternaturally elongated bregmato-mental diameter, is not quite so rare, I having the opportunity to systematically study four or five such patients in a total number of some sixty to seventy thousand cases of ophthalmic disease that I have seen in the combined public and private practice of myself and others.<sup>1</sup>

The reproduction of the photograph of the case shown in Plate XX, Fig. 2 gives a good idea of the general appearances of the head in profile. In this case the suboccipito-bregmatic circumference equaled twenty inches, the occipito-frontal circumference was nineteen and a half inches, and the occipito-mental circumference equaled twenty-six and a half inches.

CASE II.—The patient, who was born in Germany, was a thirty-five-year-old farmer. He stated that he had always had a curiously shaped skull. He had been free from all disease until he was ten years old, at which time he had had a series of spasms. These convulsions were associated with a permanent divergence of the eyes and a persistent indifferent vision which was more pronounced in the left eye. Three weeks before I saw him, he noticed that the sight of his good eye began to fail, this failure being associated at times with deeply seated orbital pains on the same side. His habits, he said, were good, and there were not any signs of gross hereditary or acquired disease. No other members of his family "for three generations back had gone blind." His parents were not blood relations.

Vision with the right eye was reduced to an intractable one-eighth of normal in an excentrically placed field, with its fixation-point situated far up and in. Color perception for green, red, blue and yellow was lost. Vision with the left eye was almost gone, there being but one small area of doubtful at times light-perception situated in an extreme temporal field as the last remnant of sensory functioning. Intraocular tension in each eye was normal. The pupil of the left eye, which was round, was about two millimeters larger than the similarly shaped one of the right eye. The right iris responded fairly well to light-stimulus and accommodative efforts, giving rise to rather prompt consensual reactions of the iris of the almost blind left eye during both of these

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St. Christopher's Hospital, in Philadelphia, for photographing the second case; to Dr. William L. Zuill, one of the Assistant Surgeons at Wills' Hospital, for the craniometric measurements of the second case; and to Dr. Frank R. Harrison, of East Liverpool, Ohio, for securing the photograph of the third case.

<sup>1</sup> Individuals from two races have been purposely used in the elucidation of this phase of the subject in order to obtain exceptionally broad standpoints of observation.

impulses. The left iris was almost immobile to light-stimulus thrown upon its retina, but responded feebly to forced movement for supposed accommodation, and gave quite prompt consensual reaction to the iris of the less affected organ. Gross downward convergence of the two eyes, by having the patient endeavor to look at his nose tip, rapidly brought the pupillary areas down to one millimeter each in size.

In spite of a left divergence of about thirty degrees out and slightly down, the exterior muscles of the two organs seemed to enjoy good movement. An almost constant lateral nystagmus that increased upon attempts at near fixation was a prominent symptom.

The patient's eye-grounds were characteristic of consecutive atrophy, that of the right eye showing evidences of a recent optic neuritis of postocular type.

Although not hoping for any permanency of result, I gave the patient the benefit of therapeutically driving more blood through the half-starved and degenerating neural tissues of the affected optic nerves. This was done by the internal administration of large and frequently repeated doses of strychnia, resulting in a temporary betterment.<sup>1</sup>

The main disturbances upon the visual apparatus in this case, therefore, which were probably of twofold character—meningitic and mechanical—were mainly exerted upon the optic nerves at the optic foramina. Secondary degeneration changes were only too certain, as later proven by the steady decline of vision in spite of all constitutional treatment that could be conscientiously and judiciously directed against any supposed dyscrasia.

The scaphocephalic type of cranial malformation exhibits a boat-shaped form of deformity of the cranium, with an extremely broad forehead. The deformation is dependent upon a premature union of the sagittal suture between the medial margins of the parietal bones. Here the brunt of the disturbance seems to exert itself upon the median posterior portion of the anterior fossa, the limbus of the lesser wing of the sphenoid bone, and the anterior medial portion of the middle fossa. True optic neuritis with consecutive atrophy; prominent, sightless and divergent eyes; pupils partly dilated, and irides fixed to light-stimulation, are the most prominent eye-symptoms in such cases. Intelligence is but fair, convulsive seizures are not infrequent, and a lethal ending from some ordinarily innocuous disease is most frequently an early event. Rapid and

<sup>1</sup> During a portion of my studies of this case the patient attended the public clinic of my friend, Dr. George C. Harlan, at the Pennsylvania Hospital. Dr. Harlan's findings and results of treatment coincided with my own.

unstable increases of intracranial pressure from ventricular disturbances are frequent, giving rise to repeated optic nerve-head swellings and retinal extravasations.

The head of the leptocephalic type is small. This condition is caused by a too early union of the fronto-sphenoidal suture between the *alæ* of the frontal and sphenoidal bones. In this type the intracranial distortions, particularly those that affect the foramina and fissures between the body and the greater and lesser wings of the sphenoid bone, bring optic nerve atrophy from previous inflammation, and later palsies of the exterior ocular muscles, into existence very soon after birth.

The trigonocephalic or three-cornered type of cranial deformity, with its small end situated anteriorly, is dependent upon a premature or improper ossification of the frontal and parietal bones along the coronal suture, particularly in the region of the bregma or pterion; or, at times, it may be due to a fault in osseous ankylosis of the combined frontal bones along the metoptic suture-line. Postneuritic atrophy, the principal ocular expression of the disease, occurring quite early in postnatal life, is apt to appear in the gross examples of the type.

The rarely seen occipital or occipito-parietal type of cranial deformity exhibits a flattened curving of the posterior portion of the cranium. The condition seems to be dependent upon either a too early syntosis of the occipital suture, especially at the lambdal region, or an improper union of the medial portion of the lambdoidal and postero-inferior part of the sagittal suture in the region of the posterior fontanelle. Here, in the superior and the posterior parts of the deepest portion of the intracranial cavity (in the interparietal parts of the occipital bone above the grooves for the lateral sinus), the osseous tissues are distorted and flattened. In certain places this condition is so pronounced, that in some situations the cerebral fossa are almost annihilated, and the inmost portion of the elevation of the superior longitudinal sinus and *falx cerebri* is increased. The most marked ocular signs are almost wholly sensory in character. Vision in each eye is nearly or entirely lost. The orbits are shallow, particularly at their postero-mesial parts. The eyeballs are but slightly proptosed, somewhat enlarged, and enjoy full freedom of movement. The motor apparatus of the exterior of the eyes, with the exception of a few minor discrepancies of probable improper nuclear action, is in good working

order. The pupils are but slightly, if at all, oversized. The irides are prompt to light-stimulus, efforts for accommodation, and convergence. The ciliary muscles are active. The eye-grounds, in every detail of neuronie, vascular, and lymph structure, appear normal; in fact, the eyeballs, with their entire adnexa, are healthy and perform their functional duties properly.

This complexus of symptoms, with its absolute blindness and concomitants of slight globular protrusion, divergence and the rotary nystagmus as the only ocular signs, constitute a most remarkable clinical picture. In it is seen a blindness, the proving of which necessitates a careful study of every possible direct and indirect ocular detail; a blindness that, from the ocular signs and associated conditions, may be assumed as intracranial in type, and most probable, until autopsy proves to the contrary, mainly cortical in character.

The accompanying reproduction of a photograph (Plate XX, Fig. 3) of a case recently studied by me and described in full elsewhere,<sup>1</sup> gives an excellent idea of the cranial deformation and the peculiar facial appearances and expression in an American-born type of case of this character. In this child the optical and receiving portions of the visual apparatus were apparently perfect. No visual perception, however, could be evolved in this case, no matter how centrally the impression reached (surely in this case back to the midbrain). Cortex sensation was lost; the discharging station was functionless.<sup>2</sup>

The cases thus far described exhibit but little, if any, mental involvement. The grossest of the resultant disturbances are mainly basilar in character, and in measure affect the vascular channels, the lymph cavities and the coarse nerve fibrils as they pass through both the primary and the secondary foramina. Trophic ocular disorder soon takes place; ophthalmic irritation signs and palsies early appear; sensory changes in the organs of vision quickly ensue; and, sooner or later, the main portions of the receiving, transmitting and discharging parts of the visual apparatus degenerate and become useless. Should the main distortions be situated in the anterior and central portions of the cranial base, producing antero-midbrain disorder, as in the first illustrative case, the more frequently in-

<sup>1</sup> The *American Journal of the Medical Sciences*, January, 1902.

<sup>2</sup> It is probable that cases of the badly termed condition "amaurotic family idiocy," with their peculiar lesions in the fundus of each eye, have some such similar origin.

volved become the ocular end organs. In this type the most bizarre motor ophthalmic signs are commingled in complicated yet definitely determinate interrelationships. On the contrary, the further back the coarse osseous changes are found, the greater become the sensory deficiencies of the visual apparatus and the better preserved remain the organs of vision and their contiguous parts.

In the anterior types the main basal cause of the condition may be summed as a series of asymmetries of basilar structures, with coarse anomalies in the various portions of the underlying sphenoidal and contiguous bones.

In the posterior types histological examination reveals cortex and nuclear changes in the posterior part of the sensory portions of the visual apparatus. In some such individuals the cellular elements may have attained a good size, and may have been able to function most excellently during early postnatal life. This can be understood when it is realized that nearly ninety per cent. of the gross volume of the brain mass is obtained during the first stage of postnatal existence; later, the association fibres and the neural cells continue to be the main factors of growth. This development, of course, exerts its influence upon the formative processes taking place in the osseous cranium.

In the majority of cases of these types there is a true tissue-sclerosis.

In deformation of the cranium occurring at a very early antenatal stage, the visual apparatus is more liable to become affected than any of the other special sense organs. On the contrary, morbid causes which affect the same apparatus during the later stages of development of the skull and its contents are not so apt to affect the organs of vision. It may be also of interest to state that the sensory portion of the visual apparatus being developed much earlier than the motor, and not possessing so many separations and ramifications in midbrain, is better able to withstand coarse pathological changes than the latter. Statistics and personal observations, however, have determined that the great majority of congenitally blind subjects possess malformations of the skull and its appendicular elements.

Far different are the grosser forms of more generalized cranial deformation, such as the two great classes, microcephales and macrocephales. Coarser disturbances of sensation, grosser peculiarities of motion, and increased degrees of trophic condition affect other



situations more markedly than they do the visual apparatus. Such cases always present mental inefficiencies and disturbances from either gross organic change or deficient development and growth in the intracranially placed tissues. Circulation of but small quantities of blood and lymph of poorly nourishing quality through the distorted and oftentimes inflamed and even contracted tissues, is seen in so many cases of this coarse type of disease, that it seems no wonder that cerebral development and growth soon become affected. Many such subjects are fortunately early victims of convulsive seizure, mental hebetude, general wasting from ectogenous infection, and death.

The cerebral alterations in these types are many. Should the case exhibit mental deficiency, the convolutions are generally gross, narrow and uncomplicated, while the related gyri are small and badly developed. Fissural confluences may be present, and not infrequently the occipital lobes do not extend over the usually too large cerebellum. These conditions are probably also found in other forms of genetous idiocy with and without eye lesions.

Some cases of that rare condition, microcephales, from too early ossification of the cranial sutures with and without idiocy, may have true microphthalmus as a part of the products of the same morbid cause; though functioning power, particularly that for color-perception, as far as can be scientifically determined, may, even in minor cases, remain practically undisturbed. As a rule, the eyeballs of such subjects are relatively well placed, and exterior ocular muscle action seems good.

In hydrocephales, on the contrary, there are frequent disturbances of muscle action in and around the eyeball, particularly during attempted movements of coördination, and when the parts are brought into association with the related ocular reflexes.

An extremely broad interpupillary distance with a broadening of the zygomatic arches forms one of the characteristic ophthalmic features of congenital cretins, whether they be endemic or sporadic in origin. In this peculiar type of cases sight is generally undisturbed, the sensory part of the visual apparatus usually being good. The visual organs, however, are somewhat differently sized. In such cases disturbances with the motor portions of the visual apparatus are quite common. The affected individuals are frequently deficient in hearing and are often unable to enunciate. The size of the orbits in these cases is unequal. The osseous irregularities,

however, are greater at the base of the skull. There is always a marked tendency to cranial asymmetry, the most pronounced abnormality consisting in a premature ossification of the sphenobasilar bones. In these cases the distance from the glabellar point to the occipital foramen is said by some to be quite short; by others this shortening is denied. Curiously, such subjects are said to never shed tears. Investigations, however, especially as to the condition of the secretory apparatus in these cases, should be made before any such dogmatic assertion as this can be hazarded.

It must be remembered that this communication does not deal with monstrosities such as cyclocephales, in which it is stated there is a circumscribed impairment of development and growth from mechanical pressure, exerted in some instances by the amniotic hood, an increase of intracranial pressure, resulting in rupture of the early cerebral vesicle, or an arrested development of the anterior vesicle as one of the results of anomalies in the amnion. This form of malformation presents several varieties. The first type of a true cyclopic monstere is that exhibiting the rhinocephalic malformation. Such an individual is represented by a head containing two more or less completely fused rudimentary eyes in a single orbit, the nose consisting in a proboscis situated above the orbit. When there is a complete fusion of the orbital cavities and eyeballs without the vestige of a nose or a proboscis, the variety receives the designative term of cyclocephalus. Should the lower part of the face be additionally affected and the integument overlying the imperfectly developed superior and inferior maxillary bones hang in folds, the condition is known as stomacephalus.<sup>1</sup>

The artificial deformation of the skull of the infant in all manner of fantastical ways, which has been practiced by many tribes throughout the world before even the time of Hippocrates, is interesting in the fact that although of necessity the three great portions of the combined visual apparatus—the receiving, the transmitting and the discharging—must in every instance have been more or less pressed upon and distorted, yet probably by reason of the distortion

<sup>1</sup> These type-forms do not strictly include the nose-headed or ethmocephalic form of monster, in which there are two eyes and two orbital cavities, the nose being represented by a proboscis that is provided with either one or two nostrils. Neither do they include the monkey-headed or cebocephalic variety, in which there are two orbital cavities and two eyeballs, but not any nose, the intra-ocular region being both narrow and flat.

having been gradually accomplished after birth, gross bulbar disturbance, blindness, faulty muscle action, and coarse atrophic disorder have not been produced, and hence remain unmentioned as ordinary consequences in such cases.

Blindness from deprivation (postnatal causes), as in the wide-world known case of Laura Bridgman, which on autopsy was found to be associated with optic nerve and optic tract atrophy and thinning of the gray matter of the occipital cortex, is also a subject for discussion elsewhere.

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## ON THE CONTINUITY OF PROTOPLASM.

BY HENRY KRAEMER, PH.D.

(Plates XXI and XXII.)

(Read April 4, 1902.)

While Schleiden<sup>1</sup> conceived each cell to have an independent existence, Hofmeister<sup>2</sup> contended that the protoplasts of contiguous cells are united, forming a higher unity; that is, one synplast. In later years both Sachs<sup>3</sup> and Strasburger<sup>4</sup> have supported the view of Hofmeister. And even so great an authority as Nägeli<sup>5</sup> expressed the view that neighboring plant cells are united by means of threads of protoplasm in much the same manner as in the sieve tubes first described by Hartig<sup>6</sup> some thirty years before.

In 1878 Thuret and Bornet<sup>7</sup> first called attention to the fact that in certain of the Floridæ the contents of certain of the cells of the trichophore and carpogonium are directly connected by means of pores. Frommann<sup>8</sup> appears first to have called attention to the direct connection of protoplasm in the higher plants, in the epidermal and parenchyma cells in the leaves of *Rhododendron* and *Dra-cena*. While Tangl<sup>9</sup> was preceded by these several investigators, the establishment of the view that there is a continuity of protoplasm is due for the most part to his researches. On treating dry sections of the endosperm of *Strychnos Nux vomica* with dilute iodine solutions, he observed a distinct lamellation of the cell wall as well as the formation of yellowish striæ, which latter he conceived to be plasma threads connecting the different cells. The appearance thus produced he compares to the structure of the sieve tubes, but in speaking of the contents of the latter, he states that

they can hardly be considered to be in the nature of protoplasm, and substantiates this statement by quoting from De Bary and Sachs.

A few years later Gardiner,<sup>10</sup> while working in the laboratory of Sachs on certain sensitive plants, observed by the use of sulphuric acid or chlor-zinc-iodide and Hofmann's blue or methylene blue, colored striæ in the walls of certain of the cells, which he considered to be in the nature of threads of protoplasm. A number of other workers have also considered this subject, using a similar technique to that of Gardiner, confirming his observations and extending the number of species showing a continuity of protoplasm.

The results obtained by these investigators tend to show that there are two kinds of continuity of protoplasm, one through openings in the pores which apparently occur in the larger number of cases, and another in which the threads of protoplasm extend through walls in which there are no pores. Several investigators<sup>11</sup> even go so far as to express the view that probably every cell is connected with its neighboring cells by protoplasmic threads.

That there is a continuity of protoplasm has become almost a fundamental principle in botany, it being considered necessary in the transmission of irritation currents and in the distribution of protoplasm and such bodies as starch grains and oil globules, intact and quickly from cell to cell.

While fully cognizant of the plausible arguments which have been advanced in favor of the continuity of protoplasm, and, furthermore, not desiring to consider the subject theoretically, by the discussion of certain facts in regard to solution, osmosis, the ascent of sap, and other physical phenomena that might more favorably assist the plant in its various functions than a protoplasmic connection between the cells, the author presents herewith some of the results of his studies on the structure of the starch grain and cell wall, in the belief that they will throw some additional light on the subject under consideration.

Suffice it to say that these results seem to offer a different explanation for the phenomena observed by the investigators already mentioned, in their studies on the continuity of protoplasm. In other words, the appearances described by these authors as indicating a continuity of protoplasm are due to a peculiarity in the structure of the cell wall, which is made manifest by the reagents

employed and which bears an analogy to the structure of the starch grain.

In the author's studies on the starch grain, the following observations have been made :

(1) The illustrations of potato starch in the various text-books show two kinds of grains, one with the point of growth and the alternate lamellæ light in color, as figured by Sachs (Plate XXI, Fig. 1), and the other with the point of growth and alternate lamellæ dark, as figured by Strasburger (Fig. 2). This appearance, however, is not due to a difference in the grains, but is brought about by the manner of focusing on them. In the figure given by Strasburger the lamellæ are viewed from above, while in the figure of Sachs the view is from below.

(2) On treating the starch grain with water at different temperatures and a number of reagents,\* a radiating crystal-like structure is observed in the successive layers (Fig. 5). This crystalline structure appears to be most pronounced in the layers alternating with the point of growth, and is succeeded by the formation of a number of clefts or fissures (Figs. 6 and 7). In potato starch these clefts are more or less feather-like in appearance, and extend from the point of growth through the middle of the successive layers to the periphery of the grain. In wheat starch the fissures extend radially from near the point of growth to near the periphery.

(3) On treating starch grains with weak aqueous solutions of various aniline dyes, as gentian violet, eosin and safranin, it is observed that the layers which are less crystalline or colloidal in character take up the stains (Figs. 3, 4 and 7). The various clefts and fissures produced in the grains behave toward staining reagents much like the colloidal layers, and they are probably the tracts or channels through which liquids are distributed throughout the grain.

(4) We further find that these two kinds of layers behave differ-

\* The reagents used were the following: (1) Chromic acid solution (5 to 15 per cent.); (2) Calcium nitrate solution (5 to 30 per cent.); (3) Potassium hydrate solution (one-tenth of 1 per cent.); (4) Sulphuric acid (10 per cent.); (5) Silver nitrate solution (2 per cent.); (6) Sodium acetate solution (50 per cent.); (7) Potassium nitrate solution (saturated); (8) Potassium phosphate solution (saturated); (9) Hydrochloric acid (5 per cent.); (10) Potassium iodide solution (1 to 10 per cent.); (11) Tannic acid solution (5 to 15 per cent.); (12) Saliva; (13) Taka-diastase (saturated solution); (14) Chlor-zinc-iodide solution; (15) Chloral iodine solution and iodine water, equal parts.

ently toward iodine; the one rich in crystalloidal substance becomes blue with iodine, whereas the other is not affected by this reagent.

In the studies of the author on the structure of the cell wall, the following observations tending to show an analogy to the starch grain have been made:

(1) A similar layering of the cell wall, known as stratification and striation, is readily observable in the walls of endosperm cells as well as those cells impregnated more or less with mucilage, lignin, cutin, suberin and allied substances. In some cases the use of reagents, as acids and alkalies, may be necessary to bring out this structure (Fig. 8). While it is not always easy to determine the nature of the successive layers in the wall, still the structure seems to correspond in the main to that of the starch grain, the middle lamella of the cell corresponding to the point of growth.

(2) The same kind of reagents, but in stronger solutions, may be used to bring out the crystalline or spherite structure in the walls of thickened parenchyma cells, as endosperm (Plate XXII, Figs. 9 and 13), or lignified cells, as stone cells. In cases where the cell wall has been metamorphosed into mucilage, simple treatment with water, as has also been shown to be the case with the starch grain, is sufficient to bring out this structure.

(3) The differentiation of the layers of the cell wall by the use of aniline stains,\* has not as yet been attended with any marked degree of success. The use of swelling reagents, as sulphuric acid, in conjunction with a stain, has, however, produced more or less interrupted striæ resembling the clefts and fissures in the starch

\* The methods involving the use of aniline stains in the study of the cell wall are the same as those used in the study of the continuity of protoplasm, and embody the three operations of fixing, swelling and staining, between each of which operations the sections are washed quickly and with large quantities of water. Fixing is usually accomplished by the use of aqueous iodine solutions (.5 per cent. of iodine and .5 to 1 per cent. of potassium iodide); alcohol, osmic and picric acids may also be employed. The swelling of the specimens is effected by the use of dilute sulphuric acid (25 to 75 per cent.), iodine being sometimes added to the sulphuric acid solution; chlor-zinc-iodide and solutions of the alkalies are also employed for this purpose. The stains mostly employed are 5 per cent. aqueous solutions of gentian-violet, eosin or safranin, these being used in connection with the swelling agents mentioned above. The time required for each operation is usually from five to ten minutes, but when chlor-zinc-iodide is used twelve hours may be required for the swelling.

grain. In the case of *Nux vomica*, solutions of potassium iodide and iodine produce yellowish-brown striæ in fresh sections (Fig. 13), closely resembling in form those produced by aniline stains (Fig. 14), and which were considered by Tangl as being protoplasmic threads, but which are probably due to the precipitation of an alkaloidal salt in the clefts or fissures in the wall.\*

(4) The two kinds of layers behave differently toward chlor-zinc-iodide; the one next to the middle lamella and those alternating with it are colored blue, while the others are but slightly affected.

The observations and comparisons herewith presented lead to the following interpretations:

(1) The starch grain, as also the cell wall, is made up of alternate lamellæ of colloidal and crystalloidal substances.

(2) Physically, the structure of the starch grain and cell wall are quite similar, although chemically different; the preponderating substance in the starch grain being granulose, while in the cell wall the fundamental substance is cellulose, which may preponderate or exist in varying proportions.

(3) The crystalloidal layer in the starch grain, consisting chiefly of granulose, is colored blue with iodine or chlor-zinc-iodide, whereas in the cell wall this layer, consisting chiefly of cellulose, is colored blue only with chlor-zinc-iodide.

(4) The colloidal layers in both the starch grain and cell wall take up and hold various aniline dyes, the layers being, however, more clearly defined in the starch grain, particularly potato starch.

(5) In starch grains as in cell walls, there are radial clefts or colloidal areas which under certain conditions also take up and hold various aniline stains.

(6) The plastid at the periphery of the starch grain may be compared to the protoplasm of the plant cell, each contributing to the growth of successive new layers. In the cell wall the mode of growth is centripetal, whereas in the starch grain it is centrifugal.

The peculiar bi-convex arrangement of the groups of striæ between contiguous cells in the *Nux vomica* and vegetable ivory is rather suggestive of fundamental lines of development corresponding to chromatin threads, although they may be modifications of the wall

\* This may explain why the iodine method alone has not met with any success save in the case of fresh sections of *Nux vomica*.

and represent tracts or channels through which liquids are distributed from cell to cell.

Furthermore, attention should be directed to the fact that the preparations of both the starch grain and cell wall showing the colored lamellæ and striæ, as already described, are permanent only in Canada balsam and are ephemeral in glycerin or glycerin jelly.

Finally, it may be stated that all authors since the appearance of Gardiner's work \* have fallen into the error of supposing that a certain aniline dye could be regarded as a differential stain for protoplasm, whereas the fact of the matter is that many colloidal carbohydrates, as mucilage and pectin, and oils and other substances as well, take up these stains. And in this connection we may ask, If the substance in the cell wall which takes up the stain is protoplasm, what is it in the starch grain?

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#### EXPLANATION OF PLATES.

##### PLATE XXI.

Fig. 1. Potato starch grain with point of growth and alternate lamellæ light in color.

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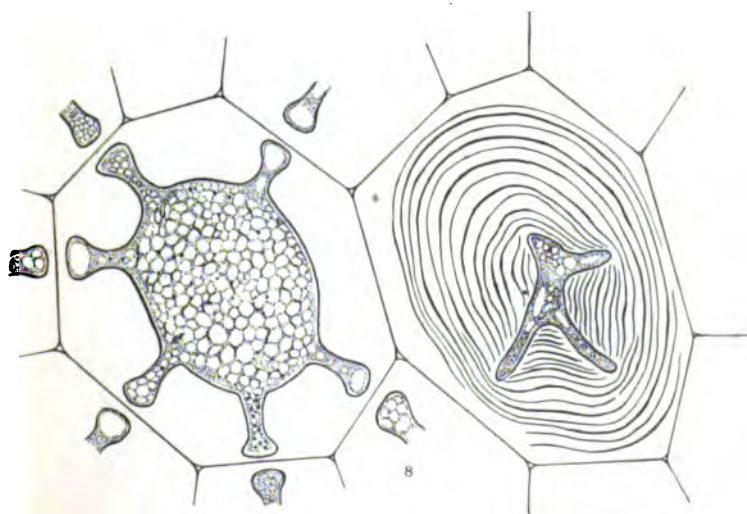
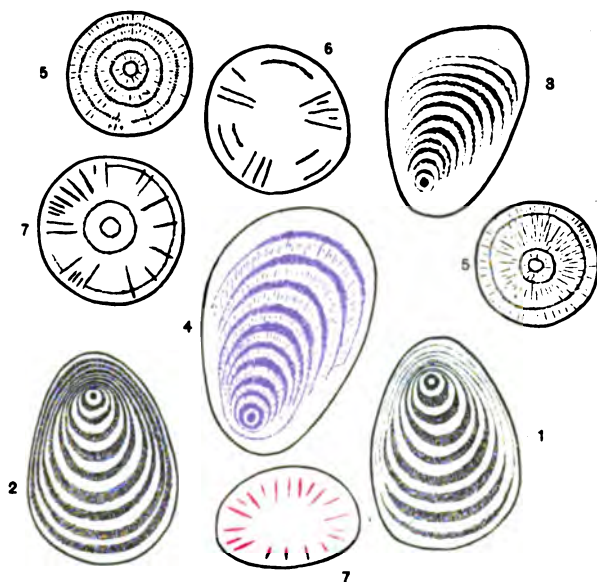
\* Gardiner states that "All experiments made with the view of attempting to detect the presence of protoplasmic filaments in the cell wall when the cell was normal and intact met with but little success, so that in investigating the subject of protoplasmic continuity the method of swelling the cell wall and subsequently staining with a dye which was found to especially stain the protoplasm was adopted."



- Fig. 2. Potato starch grain with point of growth and alternate lamellæ dark.  
Fig. 3. Potato starch grain treated with aqueous solution of gentian violet.  
Fig. 4. Potato starch grain treated with gentian violet and showing crystalloidal structure in alternate lamellæ.  
Fig. 5. Wheat starch grain treated with water at 60° C., or with chromic acid and other reagents (see footnote \*).  
Fig. 6. Wheat starch grain treated with water at a temperature of 65° C., or with the reagents mentioned in footnote \*, but for a longer time.  
Fig. 7. Wheat starch grain treated with aqueous safranin solution.  
Fig. 8. Cells of the endosperm of Date seed (*Phoenix dactylifera*), the one normal and the other showing the stratification of the wall after treatment with chlor-zinc-iodide.

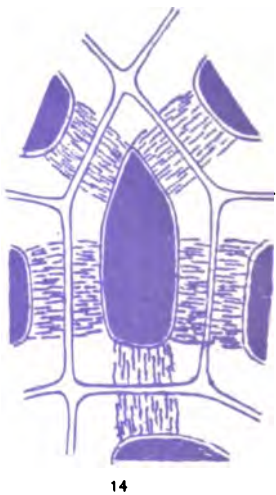
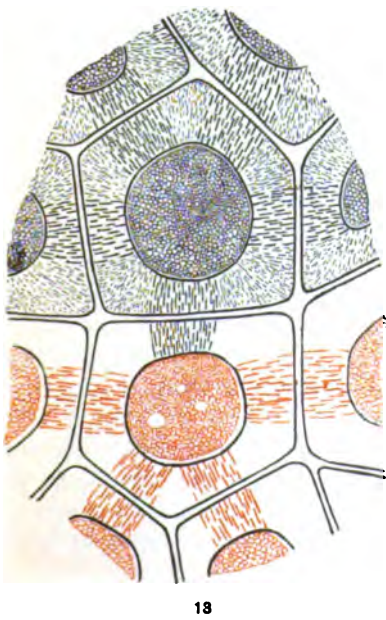
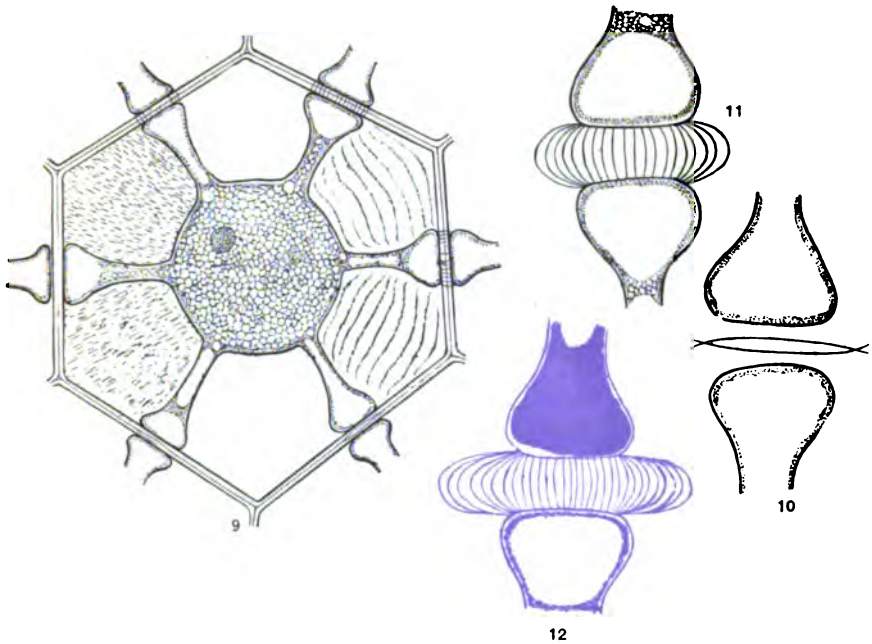
## PLATE XXII.

- Fig. 9. Cell of vegetable ivory (*Phytolophas macrocarpa*), showing lamellation and crystalline structure in the wall after treatment with chlor-zinc-iodide, clove oil, chromic acid or other reagents.  
Fig. 10. Pore of vegetable ivory showing cleft in middle lamella.  
Figs. 11 and 12. Pores of vegetable ivory showing striæ between neighboring cells after treatment with sulphuric acid and gentian violet.  
Fig. 13. Cells of endosperm of the seed of *Strychnos Nux vomica* after treatment with iodine solution.  
Fig. 14. Cell of endosperm of seed of *Nux vomica* treated with sulphuric acid and gentian violet.

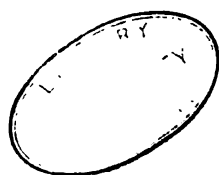


KRAEMER—THE CONTINUITY OF PROTOPLASM.





KRAEMER—THE CONTINUITY OF PROTOPLASM.



## ON SOME EQUATIONS PERTAINING TO THE PROPAGATION OF HEAT IN AN INFINITE MEDIUM.

BY A. STANLEY MACKENZIE.

(Plates XXIII-XXVIII.)

*(Read April 4, 1902.)*

We may attack a problem in the theory of the conduction of heat in two ways; we may make use of a Fourier's series or integral, or, since the general differential equation is a partial linear one, we may build up the required solution out of known solutions for simpler cases. The former way is usually much the more expeditious if the proper "trick" can be hit upon, but the method is a purely artificial one, throwing no light on the process involved. The student or reader sees at once that this method produces the required result and that a limited number of very similar problems might be treated in the same way, but he is apt to feel instinctively at first that the mathematical tool he has employed is one of which he has only a superficial knowledge and that will fail him when he gets out of a certain set of problems; he wonders what a Fourier's integral means and why it has a special value in such problems. The trouble here, as in many other departments of physics, is that the physical interpretation of mathematical operations is usually avoided. There can be but one good reason for this, since all must admit the desirability of such interpretations, that it is at times exceedingly difficult, if not impossible, to give the inherent physical meaning of a mathematical operation. Much more, however, might be done than is done, and there is perhaps no branch of mathematical physics more suited to the purpose of introducing to those just beginning such studies the meanings and the limitations of mathematical operations than heat conduction. The second method of treating heat conduction problems, by building up solutions from known solutions for other cases, is full of suggestiveness, and brings into view the meaning of many of the mathematical processes employed in any treatment of the conduction of heat, and the relationships of the equations involved. An attempt is made in the following pages to point out the necessity for effort along the lines indicated above, and among other things to give careful drawings of some of the more important curves of temperature and current.

In any heat conduction problem we have ordinarily three sets of equations, the general differential equation, the initial conditions, and the surface conditions. For the general purposes of this paper by taking the medium infinite we can get rid of the surface conditions without limiting the generality of the methods. Suppose we wish to study the case of a body of any shape or size maintained at any temperature in an infinite homogeneous medium of the same material as the body itself but initially at a uniform low temperature (which for convenience we take as the zero of temperature), or of the same body at a given initial temperature put into the medium and left to cool, we could find their solutions by an ordinary summation if we knew those for the corresponding problems in the case of an infinitesimally small particle. We might begin by assuming as Kelvin does (*Math. and Phys. Papers*, Vol. ii, p. 44), the solution for the case of a quantity of heat,  $Q$ , suddenly generated at a point  $r = 0$  at time  $t = 0$ ; but it will be better to see if it can be derived.

We have here to deal with the case of a symmetrical distribution of temperature about a point. The form of the general differential equation for this case is

$$\frac{1}{k} \frac{\partial V}{\partial t} = \frac{2}{r} \frac{\partial V}{\partial r} + \frac{\partial^2 V}{\partial r^2}, \dots\dots\dots(1)$$

where  $k = \frac{K}{CD}$ ,  $K$  being the specific conductivity,  $C$  the specific heat, and  $D$  the density of the medium. This equation can be put in the more symmetrical form

$$\frac{1}{k} \frac{\partial (Vr)}{\partial t} = \frac{\partial^2 (Vr)}{\partial r^2} \dots\dots\dots(2)$$

This is of exactly the same form as that for the case of the "linear flow of heat" of Fourier, that is, of flow in one dimension only, namely,

$$\frac{1}{k} \frac{\partial V}{\partial t} = \frac{\partial^2 V}{\partial x^2} \dots\dots\dots(3)$$

The distribution of  $Vr$  with reference to  $r$  for the case of symmetry about a point is the same as the distribution of  $V$  with reference to  $x$  for the case of symmetry about an infinite plane perpendicular to the axis of  $x$ . This fact will be of assistance in obtaining and translating results. The ordinary way of treating

any problem of spherical symmetry is to get the simplest kind of a solution of (1) or (2) and build up from that solution to the required one. There is of course an infinite number of solutions of these equations and a great many simple ones, but we can at once find one by trying  $Vr = e^{ar + \beta t}$ . This gives  $\beta = ka^2$ , and hence  $Vr = e^{ar} e^{-ka^2 t}$ . Changing  $a$  to  $ia$  we get  $Vr = e^{-ka^2 t} (\cos ar + i \sin ar)$ , and so a solution is

$$Vr = e^{-ka^2 t} \cos ar, \dots \dots \dots (4)$$

where  $a$  is any constant. This equation represents a periodic distribution of  $Vr$  along a radius vector dying out with the time; for the case of the infinite plane this would be actually the curve of distribution of temperature along  $x$ . It is seen that the values of  $V$  in (4) possess maxima and minima; the temperatures are zero at distances given by  $r = (2n + 1) \frac{\pi}{2a}$  at all times. There is a hot central sphere of radius  $\frac{\pi}{2a}$ , surrounded by alternate hot and cold shells of common thickness  $\frac{\pi}{a}$ , the maximum numerical temperature in each falling as we go away from the centre. Calling the thickness of the shells  $d$ , we have  $a = \frac{\pi}{d}$ ; so that the constant  $a$  is inversely proportional to the thickness of the shells and determines it. The central point begins by being, and remains, infinitely hot; the hot and cold layers conduct heat to each other and gradually die down in temperature. At a great distance from the origin we should have practically the case of a medium made up of alternate hot and cold infinite plates of the same numerical temperature and the same thickness left to cool; and such a problem could be treated from a consideration of (4).

This case is far from the problem we started out to discuss. We can, however, get new solutions from the simple one above, and the common method is now to say that the following is a solution of (2),

$$Vr = \int_0^\infty e^{-ka^2 t} \cos ar \, da, \dots \dots \dots (5)$$

and then translate this equation as we have just translated (4); but



instead of doing so we ought rather to be able to say that this operation means such and such and foretell the distribution of temperature it will give. This illustrates what was meant above when saying that we ought if possible to give the physical interpretations of mathematical processes. What is the meaning of the operation involved in (5)? Perhaps some light can be had on it from the following consideration: We are to take a series of distributions of temperature like that given by (4) and described above, where the constant  $a$  (determining the thickness of the shells) has the successive values,  $0, da, 2da, \dots, a$ , and superpose them on the medium after first reducing every temperature by multiplying it by  $da$ . We are then to take  $da$  indefinitely smaller and smaller, and finally to make  $a$  indefinitely greater and greater. We have thus the difficulty of a double limit entering, and if we wish to seek the initial condition it becomes a triple limit. This is sufficient to prevent any rash prediction in this problem as to the exact nature of the solution to be obtained; and this case serves as an excellent example of the difficulties to be overcome in any such efforts at physical interpretation. Before the limit is reached the state of temperatures is given by

$$Vr = du \left[ 1 + e^{-kt(da)^2} \cos rda + e^{-4kt(da)^2} \cos 2rda + \text{etc.} \right].$$

The limiting value of this series, which is equation (5), is not very evident without considerable study, but on account of the dying-out factor in each term the series is convergent, and the more rapidly convergent the greater the value of  $t$ , and its value could be found for any given  $t$  and  $da$ . Another way of finding this value at any time and distance required is to take an axis along

which  $a$ 's are measured and draw the logarithmic curve  $e^{-kta^2}$  and the curve  $\cos ra$ , then form the curve whose ordinate at each point is the product of the ordinates of these two curves at the point, and the area between this new curve and the axis gives the numerical value of  $Vr$ . Since this area is formed of pieces alternately above and below the axis of  $a$  and of decreasing numerical value, we see that  $Vr$  is always of the same sign and that, for any finite value of  $r$ , it begins by increasing in value and finally falls off to zero, and by inference that it is zero at time  $t = 0$ ; but that at the origin it has initially a value greater than zero. The

operation (5) therefore promises at least another simple solution and one much nearer the desired one. Noting that

$$\int_{-\infty}^{+\infty} e^{-ka^2t} \cos ar \, da = 2 \int_0^{\infty} e^{-ka^2t} \cos ar \, da, \text{ and that}$$

$$\int_{-\infty}^{+\infty} e^{-ka^2t} \sin ar \, da = 0, \text{ we get } \int_{-\infty}^{+\infty} e^{-\frac{1}{2}(kta^2 - ira)} \, da =$$

$$e^{-\frac{r^2}{4kt}} \int_{-\infty}^{+\infty} e^{-\left(\sqrt{kt}a - \frac{ir}{2\sqrt{kt}}\right)^2} \, da = \sqrt{\frac{\pi}{kt}} e^{-\frac{r^2}{4kt}},$$

and (5) becomes

$$Vr = \frac{A}{\sqrt{kt}} e^{-\frac{r^2}{4kt}}, \dots\dots\dots (6)$$

where  $A$  is an arbitrary constant. This equation says that  $Vr$  is initially indeterminate (evidently infinite, from physical considerations) at the centre and zero elsewhere; as time goes on the value of  $Vr$  falls off indefinitely at the centre, rises to a maximum at all other points and then falls off indefinitely also. Now these are exactly the conditions we want for  $V$  itself for the case of an infinitely hot point cooling in an infinite medium initially of zero temperature. If we had been studying (3) we would have found the same equation as (6), with  $x$  for  $r$  and  $V$  for  $Vr$ , for an infinitely hot plane cooling in a medium initially zero. The form of the curves for  $Vr$  given by (6) is exhibited on Plates XXIII and XXIV; with values of  $r$  as abscissæ curves  $A^1$  to  $A^4$  are for values of the time  $\frac{1}{16k}$ ,  $\frac{1}{8k}$ ,  $\frac{1}{4k}$  and  $\frac{1}{2k}$  respectively; with values of  $4kt$  as abscissæ curves  $B^1$  to  $B^4$  are for values of the distance 0,  $\frac{1}{4}$ ,  $\frac{1}{2}$ ,  $\frac{3}{4}$  and 1 respectively.

We have taken the form (2) of the differential equation in preference to (1) on account of its symmetry and because we are solving the case of the infinite plane at the same time; but it possesses another important advantage. Since either form of the equation is a linear partial one we can add any number of solutions for a new solution; the question arises, therefore, whether  $V$  being a solution  $\frac{\partial V}{\partial r}$  and  $\int Vdr$  are solutions, and what are their physical

meanings. Without thinking of the special form of the differential equation, we can find the meaning of  $\frac{\partial V}{\partial r}$  as follows: Let a solution,  $V$ , be  $f(r, t)$ ; then another,  $V_1$ , is  $\frac{1}{\Delta r} f(r, t)$ , where  $\Delta r$  is a small constant; and another,  $V_2$ , is  $-\frac{1}{\Delta r} f(r, t)$ . Superpose on the medium these two states of temperature,  $V_1$  and  $V_2$ , after first displacing  $V_2$  bodily to the positive side of the origin by an amount  $\Delta r$ . When  $\Delta r$  is indefinitely decreased the limiting state of temperature is that represented by  $\frac{\partial V}{\partial r}$ , or  $\frac{\partial f(r, t)}{\partial r}$ . That is,  $\frac{\partial V}{\partial r}$  represents a heating due to a kind of doublet. We must next find out whether such a state of temperature as that represented by  $\frac{\partial V}{\partial r}$  is a solution of (1). We saw that  $\frac{\partial V}{\partial r}$  was a limiting case, and hence it is not a solution in the limit (except by some unusual accident) unless it is so just before the limit is reached. While  $\Delta r$  is still finite, but as small as we please, the superposed heatings do not satisfy the same differential equation; for  $V_1$  satisfies the equation  $\frac{1}{k} \frac{\partial f(r, t)}{\partial t} = \frac{2}{r} \frac{\partial f(r, t)}{\partial r} + \frac{\partial^2 f(r, t)}{\partial r^2}$ , while  $V_2$  satisfies the equation  $\frac{1}{k} \frac{\partial f(r - \Delta r, t)}{\partial t} = \frac{2}{r - \Delta r} \frac{\partial f(r - \Delta r, t)}{\partial r} + \frac{\partial^2 f(r - \Delta r, t)}{\partial r^2}$ , and on account of the variable coefficient these are not the same equation. Hence  $\frac{\partial V}{\partial r}$  is not a solution of (1), and is only a solution of an equation in  $V$  when that equation has constant coefficients, that is, coefficients not containing  $r$ . Equation (2) is of that kind, and hence knowing a solution of it,  $Vr$ , we can say that  $\frac{\partial(Vr)}{\partial r}$  is also a solution. Call this new solution  $V_1r$ , then  $V_1$  is a solution of (1). Since  $\frac{\partial(Vr)}{\partial r} = V + r \frac{\partial V}{\partial r}$ , and since  $\frac{1}{r} \frac{\partial(Vr)}{\partial r}$  is a solution of (1), we have  $\frac{V}{r} + \frac{\partial V}{\partial r}$  a solution of (1); this is what we have just called  $V_1$ . Now  $V$  satisfies (1), but we have just seen that  $\frac{\partial V}{\partial r}$  does not, and it can easily be seen that  $\frac{V}{r}$  does not in general; so we have the interesting fact that the solution  $V_1$  is the sum of two functions of  $V$  (itself a solution) neither of which is a solution. We can at least give a physical interpretation to the method of finding

a solution of (1) represented by the mathematical operation  $\frac{1}{r} \frac{\partial(Vr)}{\partial r}$ , where  $Vr$  is a solution of (2) and  $V$  itself a solution of (1); we have but to add to the doublet of this  $V$  as defined above a heating at each point  $r$ , which is  $V$  divided by the value of  $r$  at the point.

The meaning of  $\int V dr$ , where  $V$  is a solution of the differential equation, is now plain. It simply means finding a new function of  $r$  and  $t$ ,  $V^1$ , whose doublet is the solution  $V$ . That is,  $\frac{\partial V^1}{\partial r} = V$ , and  $V^1 = \int V dr$ . This is subject to the same limitations as before, that the differential equation for  $V$  must have its coefficients independent of  $r$ , in order that  $V^1$  may be a solution of the equation.

Similarly for equation (2); we have a solution,  $Vr$ , to find the meaning of the new solution,  $V^1r$ , which we get on performing the integration  $\int Vr dr$ . Since  $\frac{\partial(V^1r)}{\partial r} = Vr$ , or  $\frac{1}{r} \frac{\partial(V^1r)}{\partial r} = V$ , we are but finding the distribution of temperature,  $V^1$ , whose doublet added to the heating  $\frac{V^1}{r}$  gives the distribution of temperature,  $V$ , which we started with.

We thus see that (2) has the great advantage over (1) that when we find a solution of the former we can differentiate and integrate it with regard to  $r$  for new solutions, but we cannot do so with the latter.

The meaning of  $\frac{\partial V}{\partial t}$  and of  $\int V dt$  as solutions of (1) are of the same general nature as the similar expressions with  $r$ , and are quite evident; we now superpose one heating,  $\frac{1}{\Delta t} f(r, t)$  on another,  $-\frac{1}{\Delta t} f(r, t)$ , after a small interval of time  $\Delta t$ , which we make smaller and smaller indefinitely. We might call this a *time* doublet and the former a *space* doublet. Both  $\frac{\partial V}{\partial t}$  and  $\int V dt$  are solutions of (1) because the coefficients do not contain  $t$ . The same remarks apply to (2) as regards  $Vr$ , with the explanations of the former paragraph added. Here equation (2) possesses no advantage over (1).

The meaning of a Fourier's integral may now be given. A solution of (3) for the flow of heat in one dimension is evidently

$V = e^{-ka^2t} \cos \beta(a-x)$ , where  $a$  and  $\beta$  are arbitrary constants, for it is made up of  $V = Ae^{-ka^2t} \cos ax$  and  $V = Be^{-ka^2t} \sin ax$ , both of which are solutions of (3) as shown above. This equation denotes a distribution of temperatures which has maxima and minima values, the latter being at certain fixed points given by the equation  $x = a - (2n + 1) \frac{\pi}{2\beta}$ . In general it is very similar to the distribution represented by (4) already studied.  $V_1 = V\varphi(a)$  is also a solution, where the temperatures are as before except that they are increased by multiplying every one by  $\varphi(a)$ , an arbitrary constant function of  $a$ . Another solution is got, as described before, by superposing all the heatings formed on reducing the temperatures in  $V_1$  by multiplying each by the very small quantity  $da$ , and giving  $a$  all values from  $-\infty$  to  $+\infty$ , and then taking the limiting case where  $da$  tends to zero. Call this new solution  $V_2$ ;

then  $V_2 = \int_{-\infty}^{+\infty} e^{-ka^2t} \cos \beta(a-x) \varphi(a) da$ . Repeat this last operation

with regard to  $\beta$ ; that is, take the distribution of temperatures represented by  $V_2$  and reduce the numerical value of each by multiplying by  $d\beta$ , then superpose all such heatings formed by giving  $\beta$  every value from 0 to  $\infty$ , and finally take the limiting case where  $d\beta$  tends to zero. Call this new solution  $V_3$ ; then

$$V_3 = \int_0^\infty d\beta \int_{-\infty}^{+\infty} e^{-ka^2t} \cos \beta(a-x) \varphi(a) da.$$

Still another solution is got by reducing every temperature in  $V_3$  in the ratio of  $\pi$  to 1.

Call this solution  $V_4$ ; then  $V_4 = \frac{1}{\pi} \int_0^\infty d\beta \int_{-\infty}^{+\infty} e^{-ka^2t} \cos \beta(a-x) \varphi(a) da$ ;

it has the special importance and peculiarity, as was first shown by Fourier, that at time zero the distribution of temperature it represents is the same function of  $x$ ,  $\varphi(x)$ , that we took originally of  $a$ . Similarly every Fourier integral may be interpreted.

Returning now to equation (6) and the curves drawn for it, we can find new solutions by addition; at each point  $r$  let us add the temperature for that point and all other points farther from the centre, even to infinity, but first reduced in absolute value by multiplying each by the small quantity  $dr$ , which we make ultimately tend to zero. We have but to add on Plate XXIV for any

abscissa (time) the ordinates of all possible curves such as  $B^1, B^2$ , etc., below any given one, after reducing them as described. For  $t = 0$  and  $r = 0$  we would get  $(\infty + 0 + 0 + \text{etc.}) dr$ , which as  $dr$  diminishes indefinitely gives us some finite value; for other values of  $r$  we would get  $(0 + 0 + 0 + \text{etc.}) dr$ , which is zero. From the way the curves tend to become parallel it is suggested, and by trial we find, that for  $r = 0$  and any finite value of the time not zero the sum of all the ordinates would be constant. We have then the promise of another simple solution, and can foretell its type somewhat, of the form

$$Vr = \int_{-\infty}^{\infty} \frac{A}{\sqrt{kt}} e^{-\frac{r^2}{4kt}} dr = \frac{2}{\sqrt{\pi}} B \int_{\frac{r}{2\sqrt{kt}}}^{\infty} e^{-\beta^2} d\beta, \dots\dots(7)$$

where  $B$  is an arbitrary constant. On studying this equation we find that  $Vr$  at the origin has initially the value  $B$ , and maintains that value; at all other points it is initially zero and rises asymptotically with time toward the value  $B$ .  $V$  itself would be always infinite at the origin and initially zero elsewhere. For the case of linear flow equation (7) represents an infinite plane kept at temperature  $B$  in an infinite medium initially zero in temperature.

We can get the solution for an infinitely hot point put into an infinite medium initially zero and left to cool as follows: At time zero apply to the medium the state of temperatures represented by (7) with every temperature increased by multiplying it by the large quantity  $\frac{1}{\Delta t}$ ; after time  $\Delta t$  apply also the state of temperatures represented by (7) with sign changed and increased numerically as before; finally make  $\Delta t$  tend to zero. We have seen above that this is equivalent to performing the mathematical operation of differentiation of (7) with regard to  $t$ , that is, taking the time doublet of  $Vr$ . The reason that this solution is the one required is that the superposition of the two heatings gives  $Vr$  a large value at the origin at first and everywhere else a zero value, and then instantaneously makes  $Vr$  zero at the origin; that is, at the origin  $V$  is initially infinite in temperature and then falls off indefinitely, while all other points begin at zero and rise gradually. These were the conditions we wanted. Hence we have the solution

$$Vr = \frac{\partial}{\partial t} \left[ \frac{2}{\sqrt{\pi}} B \int_0^{\frac{r}{2\sqrt{kt}}} e^{-\beta^2} d\beta \right] = \frac{Er}{(kt)^{\frac{3}{2}}} e^{-\frac{r^2}{4kt}}, \dots (8)$$

and

$$V = \frac{E}{(kt)^{\frac{3}{2}}} e^{-\frac{r^2}{4kt}}, \dots (9)$$

where  $E$  is an arbitrary constant.

Further light can be thrown on this problem by arriving at equation (8) by other methods. Remembering that equation (6) gave  $Vr$  initially infinite at the centre and zero elsewhere, and falling in value at the centre and gradually rising to a maximum elsewhere, we see that by taking the space doublet of this  $Vr$  we get  $Vr$  at the origin first infinite and then zero; that is,  $V$  at the origin is at first infinite and then gradually falls off, and is initially zero elsewhere and rises with time. These are the conditions required. Hence the solution is

$$Vr = \frac{\partial}{\partial r} \left[ \frac{A}{\sqrt{kt}} e^{-\frac{r^2}{4kt}} \right] = \frac{Er}{(kt)^{\frac{3}{2}}} e^{-\frac{r^2}{4kt}} \dots (10)$$

Or we can look at it in this way: We saw that  $Vr$  in (6) had exactly the set of values we want  $V$  to have in the problem proposed, and the form of the right-hand member of (6), containing

as it does  $r$  in the factor  $e^{-\frac{r^2}{4kt}}$  only, suggests at once that we can get the desired value of  $V$  by a simple differentiation with regard to  $r$ . This is what we have just done with a good physical reason for the operation.

Or another method. We saw that equation (6) for the case of flow in one direction only was that of an infinitely hot plane cooling in an infinite medium initially zero in temperature, and to get the solution for the similar problem in three dimensions we have but to multiply that solution by two similar ones with  $y$  and  $z$  substituted for  $x$ . This gives

$$V = E \frac{1}{(kt)^{\frac{3}{2}}} e^{-\frac{x^2}{4kt}} e^{-\frac{y^2}{4kt}} e^{-\frac{z^2}{4kt}} = \frac{E}{(kt)^{\frac{3}{2}}} e^{-\frac{r^2}{4kt}} \dots (11)$$

The rate of cooling is given by the equation

$$\frac{dV}{dt} = \frac{E}{2k^{\frac{3}{2}}r^{\frac{3}{2}}} \left( \frac{r^2}{2kt} - 3 \right) e^{-\frac{r^2}{4kt}}.$$

Each point of the mass not the centre begins by being zero in temperature, then rises to a maximum after a time  $t = \frac{r^2}{6k}$ , and after this falls off indefinitely toward zero. The forms of the curves given by (9) are exhibited on Plates XXV and XXVI. With values of  $r$  as abscissæ curves I' to IV' are for values of the time  $\frac{1}{16k}$ ,  $\frac{1}{8k}$ ,  $\frac{1}{4k}$ , and  $\frac{1}{2k}$  respectively; with values of  $4kt$  as abscissæ curves 1' to 5' are for values of the distance 0,  $\frac{1}{2}$ , 1,  $\frac{3}{2}$  and 2 respectively.

The meaning of the constant  $E$  is determined by finding the amount of heat supplied initially to the hot point. We have

$$Q = \iiint CDV dx dy dz = \frac{4\pi CDE}{(kt)^{\frac{3}{2}}} \int_0^{\infty} e^{-\frac{r^2}{4kt}} r^2 dr = 8CDE\pi^{\frac{1}{2}} \dots (12)$$

If we take as our unit of heat that required to raise the mass in a unit of volume of the substance  $1^{\circ}$ , the total quantity of heat,  $\sigma$ , in these units is

$$\sigma = 8E\pi^{\frac{1}{2}} \dots \dots \dots (13)$$

We could also get the total heat by taking the integral

$$\int_0^{\infty} -K \frac{\partial V}{\partial r} 4\pi r^2 dt. \text{ We get from (12) and (13) our equation (11)}$$

in the form

$$V = \frac{Q}{8CD(\pi kt)^{\frac{3}{2}}} e^{-\frac{r^2}{4kt}} = \frac{\sigma}{8(\pi kt)^{\frac{3}{2}}} e^{-\frac{r^2}{4kt}} \dots \dots \dots (14)$$

(See Kelvin's Papers, Vol. II, p. 44.)

We cannot build up by summation the solution for the case of a body of finite dimensions from the above solution for a mathematical point. We wish to pass to a case which has a physical significance, namely, a finitely hot particle left to cool in an infinite



medium of temperature initially zero. We can get a close approximation to this problem by putting the same quantity of heat,  $\sigma$ , into a particle of volume  $\Delta v$  which we put into the mathematical point, and assuming that the state of temperature produced in the surrounding medium is the same as that due to the infinitely hot point and is given accordingly by (14). This equation will represent the real state the better the longer the time which has elapsed, in accordance with the fact emphasized by Fourier that the initial heating is of less and less importance as the time is prolonged. The closeness of the approximation for any given time and distance will be brought out later.

Let the quantity of heat supplied raise the volume  $\Delta v$  to the temperature  $V_0$ ; then  $Q = CDV_0\Delta v$ , or  $\sigma = V_0\Delta v$ ; and (14) becomes

$$V = \frac{V_0\Delta v}{8(\pi kt)^{\frac{3}{2}}} e^{-\frac{r^2}{4kt}} \dots\dots\dots(15)$$

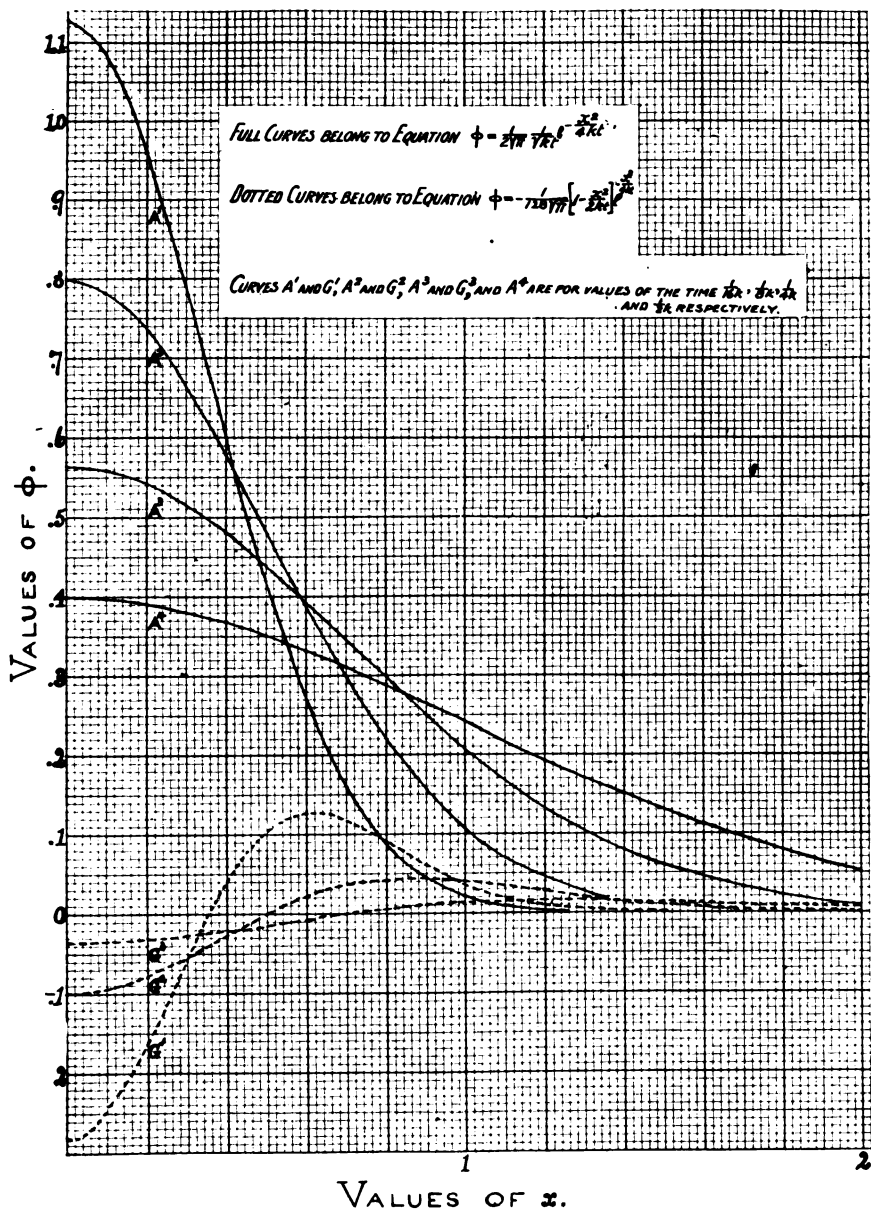
If the volume  $\Delta v$  is in the form of a sphere of radius  $R$ , (15) becomes

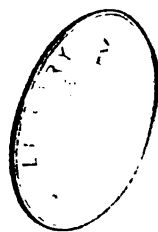
$$V = \frac{V_0 R^3}{6\sqrt{\pi}} \frac{1}{(kt)^{\frac{3}{2}}} e^{-\frac{r^2}{4kt}} \dots\dots\dots(16)$$

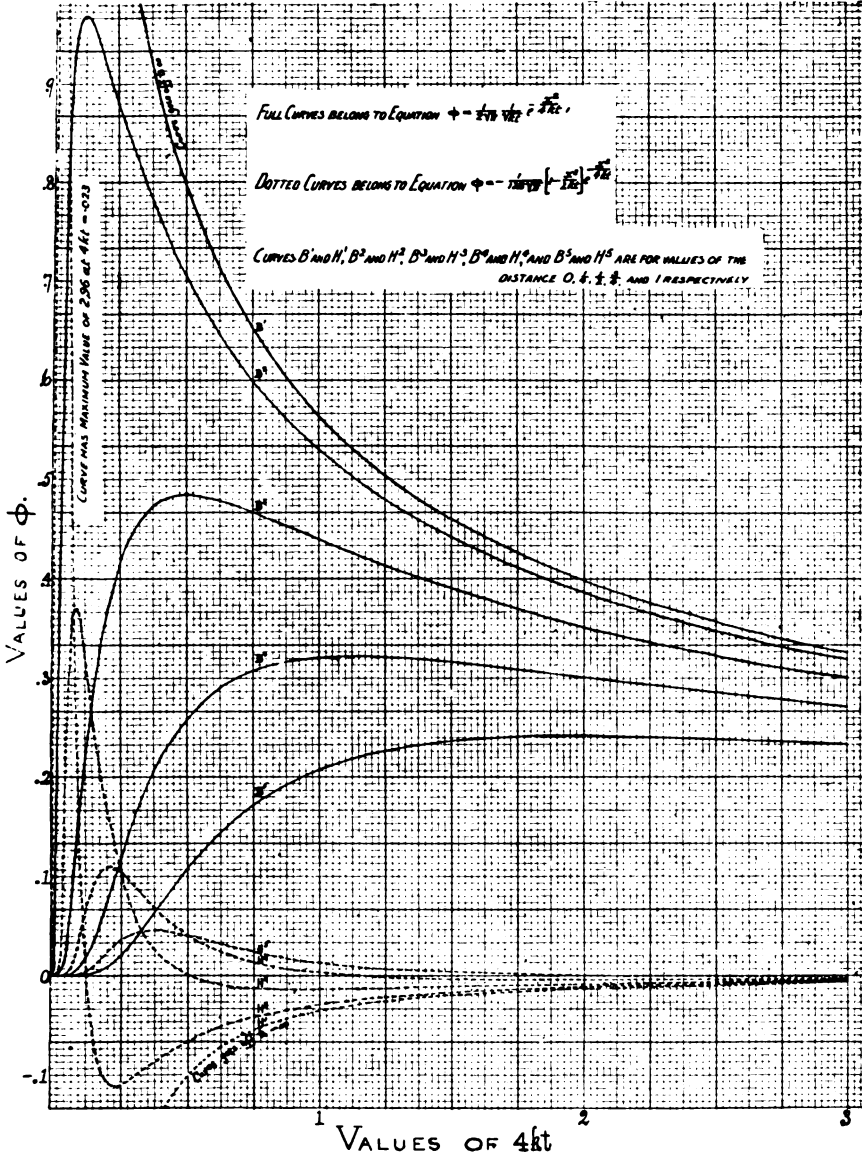
and it is really for this form of the equation, with  $R$  taken as the unit of length, that the curves referred to on Plates XXV and XXVI were drawn. They are, as said, approximations only to the true curves. The latter may be found by the aid of a Fourier's integral. We know that the solution of (2) subject to the condition  $V=f(r)$  when  $t=0$  is

$$Vr = \frac{1}{\sqrt{\pi}} \left[ \int_{-\frac{r}{2\sqrt{kt}}}^{\infty} (r + 2\sqrt{kt}\gamma) f(r + 2\sqrt{kt}\gamma) e^{-\gamma^2} d\gamma - \int_{\frac{r}{2\sqrt{kt}}}^{\infty} (-r + 2\sqrt{kt}\gamma) f(-r + 2\sqrt{kt}\gamma) e^{-\gamma^2} d\gamma \right] \dots\dots(17)$$

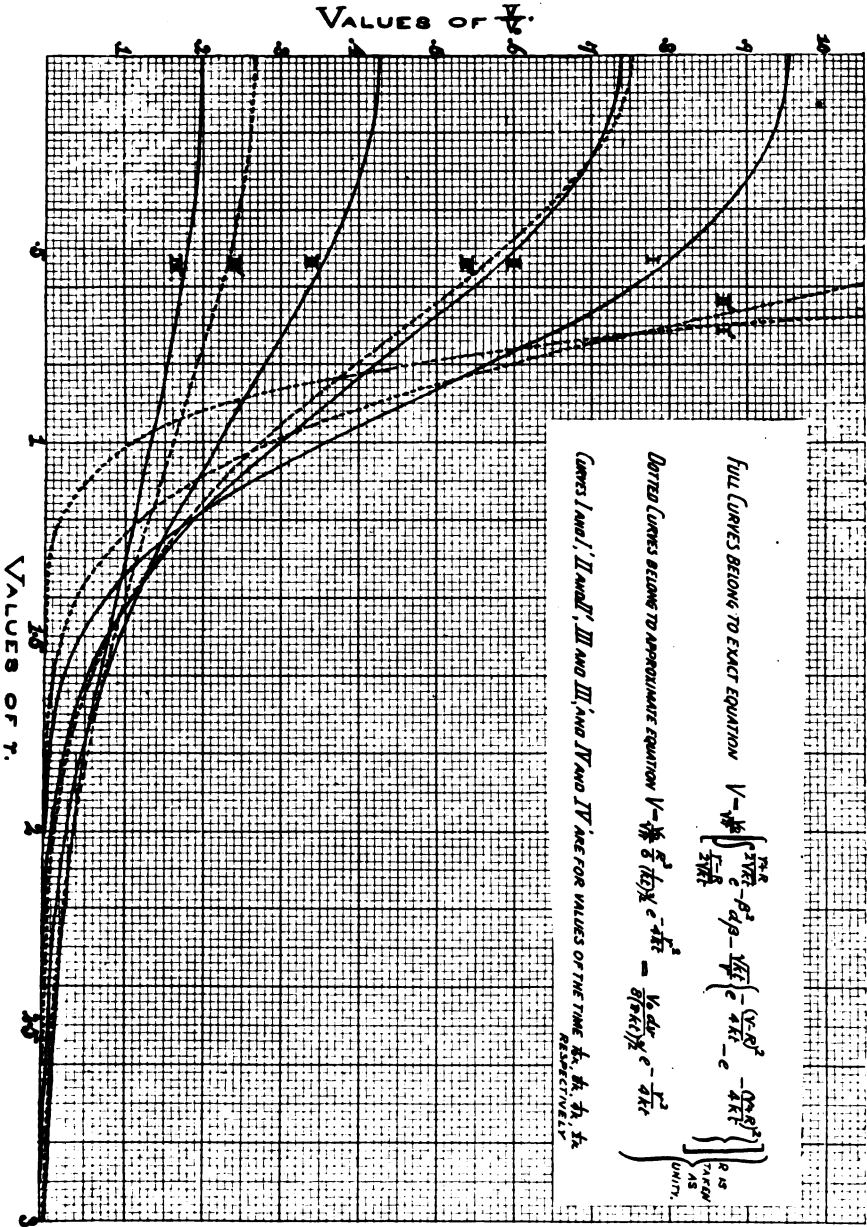
Giving  $f(r)$  the value  $V_0$  from  $r=0$  to  $r=R$ , and the value 0 from  $r=R$  to  $r=\infty$ , (17) takes the form





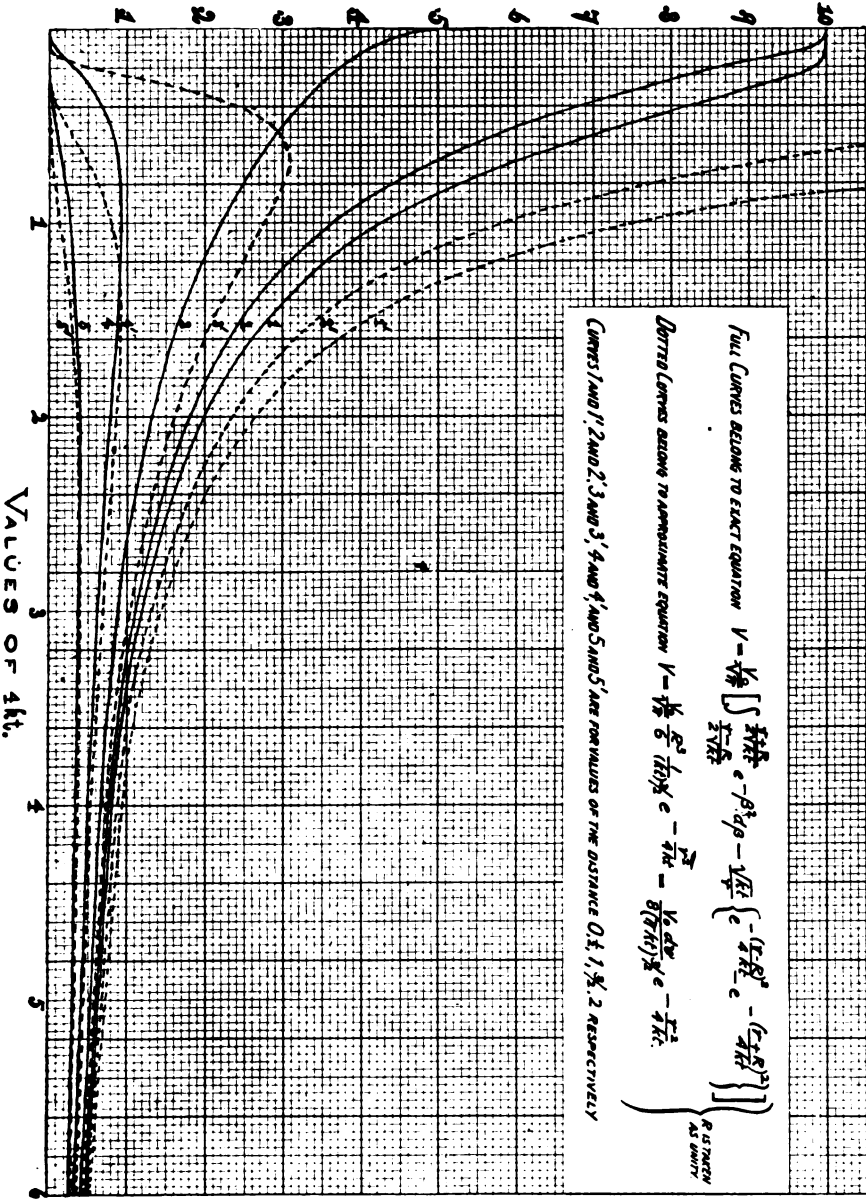








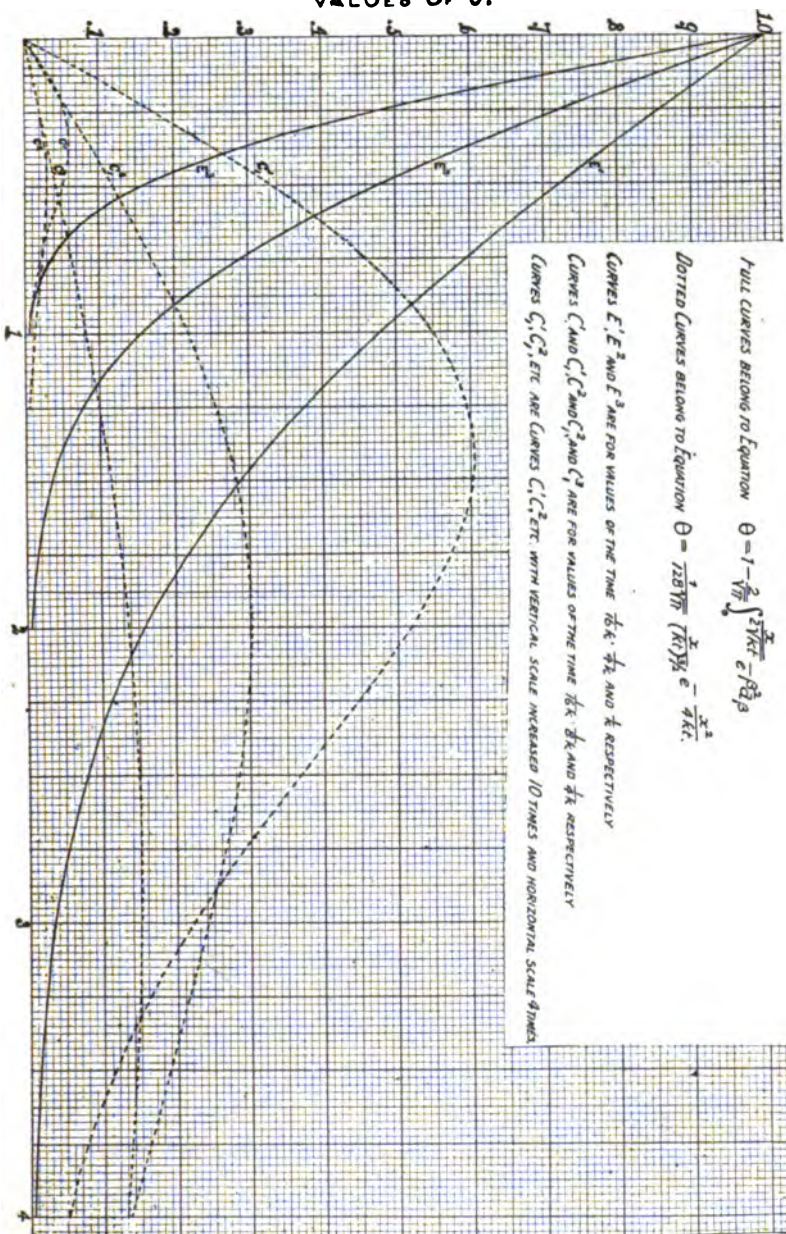
VALUES OF  $\frac{V}{V_0}$ .







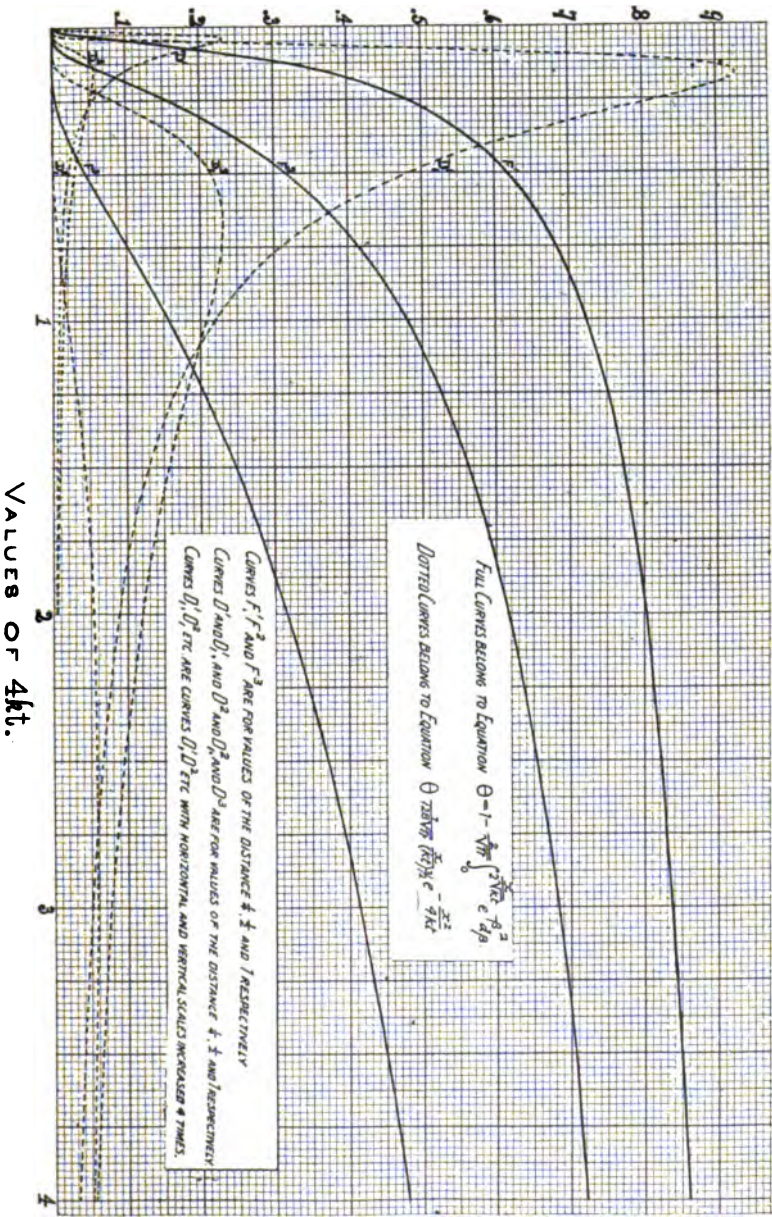
VALUES OF  $\theta$ .



VALUES OF  $x$ .



VALUES OF  $\theta$ .





$$V = \frac{V_0}{\sqrt{\pi}} \left[ \int_{\frac{r-R}{2\sqrt{kt}}}^{\frac{r+R}{2\sqrt{kt}}} e^{-r^2} dr - \frac{\sqrt{kt}}{r} \left\{ e^{-\frac{(r-R)^2}{4kt}} - e^{-\frac{(r+R)^2}{4kt}} \right\} \right] \quad (18)$$

This then is the exact equation for a sphere of any size of initial temperature  $V_0$  put into an infinite medium of the same material as the sphere of initial temperature zero and left to cool there. The forms of the curves given by this equation are exhibited on Plates XXV and XXVI, along with those of the approximate equation (16). Curves I to IV correspond to  $I^1$  to  $IV^1$ , and curves 1 to 5 correspond to  $1^1$  to  $5^1$ .

We can get an approximate form from equation (18) by expanding it in terms of  $R$ ; we find

$$V = \frac{V_0 R^3}{6\sqrt{\pi}} \frac{1}{(kt)^{\frac{3}{2}}} e^{-\frac{r^2}{4kt}} \left[ 1 + \frac{r^2}{4kt} - \frac{6}{40} \frac{R^2}{kt} \right] \dots\dots (19)$$

The first term of this is the same as equation (16), found otherwise. Equation (19) gives us a second approximation, and the second term within the bracket will enable us to determine the closeness of (16) as an approximation. In a similar problem, Fourier (Free-  
man's translation, p. 380) gives a limit to the time when the approximation may be used, but he does not give any means of telling how great the error is in general, and it was for the purpose of bringing this out distinctly that equation (19) and the curves on Plates XXV and XXVI were produced. From Plate XXV we see that the approximate curves are at first steeper and afterward flatter than the exact curves; they make the temperatures too high for points nearer the origin than a certain distance, and too low for points farther away. Indeed curves I and  $I^1$  are very little alike for any value of  $r$ . As the value of the time for which the curve is drawn is taken greater and greater the curves approach each other more and more nearly, even for points less distant than unity (which are inside the little sphere), for which we might have expected little agreement. This makes evident the fact to which Fourier calls attention at the place just cited; one is very apt to assume that the curves would approach each other more and more as  $r$  is taken greater and greater, no matter what the value of  $t$ ; but just the reverse is true,

the curves approach each other more and more for greater and greater values of the time, no matter what the distance. This is seen more distinctly from an examination of Plate XXVI. There it will be seen also that the approximate curves are slower in reaching their maximum values, as well as that they have different maxima. For distances less than unity the approximate curves start at  $\infty$ , while the exact curves start at  $V = V_0$ ; for the distance unity the exact curve starts abruptly at  $\frac{V_0}{2}$ , while the approximate curve starts at 0 then gradually rises and has a maximum value less than  $\frac{V_0}{2}$ . For distances greater than unity both curves start at the origin.

From an inspection of the second term of (19) we can foretell the approximate accuracy of (16). Taking  $R$  as the unit of length, if  $kt < 15$  the error in the value of  $\frac{V}{V_0}$  will be everywhere greater than 1% except in the immediate neighborhood of  $r = \sqrt{6kt}$ , at which point the error is practically zero. For instance, for  $kt = \frac{1}{2}$  (curves IV and IV') the approximate curve is 33% too high at  $r = 0$ , 22% at  $r = 1$ , correct at about 1.8, and 38% too low at 3. If  $kt = 15$ , the error is not more than 1% from  $r = 0$  to  $r = 13.4$ . If  $kt = 25$  the error is not more than 1% from  $r = 0$  to  $r = 20$ . In general, for any value of  $kt$  the error is not more than 1% from  $r = 0$  to  $r = \sqrt{6kt} + \frac{2}{3}(kt)^{\frac{1}{2}}$ , and from  $r = 0$  to  $r = \sqrt{6kt}$  the error decreases gradually from  $\frac{15}{kt}\%$  to zero, and after that increases again. If we want results accurate to .01%,  $kt$  must be at least 1500, and in general for any value of  $kt$  greater than this the error is not more than .01% from  $r = 0$  to  $r = \sqrt{6kt} + \frac{1}{25}(kt)^{\frac{1}{2}}$ , and from  $r = 0$  to  $r = \sqrt{6kt}$  the error decreases gradually from  $\frac{15}{kt}\%$  to zero, and after that increases again.

From equation (15) we can build up by summation the equation for the case of a body of any shape or size initially at  $V_0$  cooling in an infinite medium initially zero. In order to bring out a very interesting difference between summation and integration we shall apply equation (15) to the case of an infinite space, one-half of which is initially at  $V_0$  and the other half at zero, the two parts being separated by an infinite plane surface. We shall first have to find the solution for a plane lamina. Take the central plane of the lamina as the plane of  $yz$ , and the origin where a perpendicular



from the point  $P$ , at which we want to know the temperature, meets this plane. Call the length of this perpendicular  $x$ . Break up the lamina into concentric rings of radius  $\rho$  about this origin, and let the distance of every point in one of such rings from the point  $P$  be  $r$  and the thickness of the lamina  $\Delta x$ ; then we have

$$V = \frac{V_0}{8(\pi kt)^{\frac{1}{2}}} \int_0^\infty e^{-\frac{x^2 + \rho^2}{4kt}} 2\pi\rho \Delta x \cdot d\rho = \frac{V_0 \Delta x}{2(\pi kt)^{\frac{1}{2}}} e^{-\frac{x^2}{4kt}} \dots\dots\dots (20)$$

From the symmetry of the problem this is evidently a case of linear flow, and the solution must satisfy equation (3). Knowing this solution (we can get it otherwise), the solution for three dimensions given in (15) can be deduced; we have but to multiply the value of  $\frac{V}{V_0}$  for the case of one dimension by two similar expressions with  $y$  and  $z$  respectively substituted for  $x$ .

The corresponding electrical problem is that of an infinite cable with no lateral loss by leakage touched for an instant to a condenser of potential  $V_0$ . If there is lateral leakage equation (20) is still the solution of the electrical problem;  $V$  is then not the potential, but the potential can be derived easily from it, as is well known.

If  $Q$  or  $\sigma$ , according to the unit of heat used, is the amount of heat required to raise the mass of a section of the plate of unit area by  $V_0$  degrees, then  $Q = CDV_0 \Delta x$ , or  $\sigma = V_0 \Delta x$ , and equation (20) becomes

$$V = \frac{Q}{2CD(\pi kt)^{\frac{1}{2}}} e^{-\frac{x^2}{4kt}} = \frac{\sigma}{2(\pi kt)^{\frac{1}{2}}} e^{-\frac{x^2}{4kt}} \dots\dots\dots (21)$$

Of course this equation is of only the same grade of approximation as (15). It will be the more nearly exact the smaller  $\Delta x$  and, since the product of  $V_0$  and  $\Delta x$  measures the heat in a section of unit area and is to remain constant, the greater  $V_0$ . In the limit we should have the solution for an infinitely hot plane. The form of this solution we have already found; it is from (6) and the remarks following it

$$V = \frac{A}{\sqrt{kt}} e^{-\frac{x^2}{4kt}} \dots\dots\dots (22)$$

Calling  $Q$  the total heat associated initially with a unit of area of



the plate, we find  $Q = 2 \int_0^{\infty} CDV dx = 2ACD\sqrt{\pi}$ ; and this value of  $A$  reduces (22) to the form (21). Hence the general form of equation (21), which is approximate for a plate of actual thickness  $\Delta x$ , is exact for the infinitely hot plane. We shall revert to this important fact later.

If we want the exact equation for the plate of thickness  $\Delta x$  we can get it by the use of a Fourier integral. Making the obvious changes in (17) to suit it to the case of linear flow, and giving  $f(x)$  the value  $V_0$  from  $x = -\frac{\Delta x}{2}$  to  $x = \frac{\Delta x}{2}$  and the value 0 for all other values of  $x$ , we find

$$V = \frac{V_0}{V\pi} \int_{-\frac{x+\frac{\Delta x}{2}}{2\sqrt{kt}}}^{\frac{x-\frac{\Delta x}{2}}{2\sqrt{kt}}} e^{-\gamma^2} d\gamma \dots\dots\dots (23)$$

Putting this in an approximate form, we have

$$V = \frac{V_0 \Delta x}{2(\pi kt)^{\frac{1}{2}}} e^{-\frac{x^2}{4kt}} \left[ 1 + \frac{x^2}{kt} - \frac{2}{96} \frac{(\Delta x)^2}{kt} \right], \dots\dots\dots (24)$$

the first term of which is equation (20). The forms of the curves for (20) are exhibited on Plates XXIII and XXIV. With values of  $x$  as abscissæ curves  $A^1$  to  $A^4$  are for values of the time  $\frac{1}{16k}$ ,  $\frac{1}{8k}$ ,  $\frac{1}{4k}$  and  $\frac{1}{2k}$  respectively; with values of  $4kt$  as abscissæ curves  $B^1$  to  $B^4$  are for values of the distance 0,  $\frac{1}{4}$ ,  $\frac{1}{2}$ ,  $\frac{3}{4}$  and 1 respectively. The second term of (24) enables us to tell approximately the degree of closeness of (20) to the exact equation (23). Taking  $\Delta x$  as the unit of length, if  $kt < \frac{25}{12}$  the error will be everywhere greater than 1% except in the neighborhood of  $x = \sqrt{2kt}$  where it is practically zero. If  $kt = \frac{25}{12}$  the error is not more than 1% from  $x = 0$  to  $x = 2.9$ , being 1% too high at  $x = 0$ , zero at  $x = 2$ , and 1% too low at  $x = 2.9$ . If  $kt = 25$  the error is  $\frac{1}{2}\%$  too high at  $x = 0$ , zero at 7, and 1% too low at 26. This is then a nearer approximation than the one discussed for the case of a hot particle, as was to

be expected. In general, for any value of  $kt$  the error is not more than 1% from  $x=0$  to  $x=\sqrt{2kt} + \frac{24}{25}(kt)^{\frac{1}{2}}$ , and for any value of  $kt$  greater than  $\frac{2500}{24}$  the error is not more than .01% from  $x=0$  to  $x=\sqrt{2kt} + \frac{24}{2500}(kt)^{\frac{1}{2}}$ ; from  $x=0$  to  $x=\sqrt{2kt}$  the error decreases gradually from  $\frac{25}{12kt}\%$  to zero, and after that increases again.

The correspondingly approximate equation for the current or flow of heat in this case is

$$I = -K \frac{\partial V}{\partial x} = \frac{KV_0 \Delta x}{4\sqrt{\pi}} \frac{x}{(kt)^{\frac{1}{2}}} e^{-\frac{x^2}{4kt}} = \frac{K\sigma}{4\sqrt{\pi}} \frac{x}{(kt)^{\frac{1}{2}}} e^{-\frac{x^2}{4kt}} \dots (25)$$

The forms of these curves are given on Plates XXVII and XXVIII. With values of  $x$  as abscissæ curves  $C^1$  and  $C_1^1$ ,  $C^2$  and  $C_1^2$ , and  $C_1^3$  are for values of the time  $\frac{1}{16k}$ ,  $\frac{1}{8k}$  and  $\frac{1}{4k}$  respectively; with values of  $4kt$  as abscissæ curves  $D^1$  and  $D_1^1$ ,  $D^2$  and  $D_1^2$ , and  $D_1^3$  are for value of the distance  $\frac{1}{4}$ ,  $\frac{1}{2}$  and 1 respectively.

The exact equation for the flow, found from (23), is

$$I = \frac{KV_0}{2(\pi kt)^{\frac{1}{2}}} \left[ e^{-\frac{(x-\frac{1}{2}\Delta x)^2}{4kt}} - e^{-\frac{(x+\frac{1}{2}\Delta x)^2}{4kt}} \right], \dots (26)$$

the curves for which have not been drawn.

By adding up the effects of an infinite number of such plates we can get the temperature due to one-half of space initially at a uniform temperature  $V_0$  and the other half at zero temperature. Take the point  $P$ , at which the temperature is desired, in the cold half and at a distance  $x$  from the surface of separation, and take the origin in that surface at the foot of the perpendicular from  $P$ . Let one of the plates making up the other half of the medium be distant  $\xi$  from the origin. Then the  $x$  of equation (20) becomes  $x + \xi$ , and  $\Delta x$  becomes  $\Delta \xi$ ; hence the temperature at  $P$  due to a series of such plates extending from  $\xi = 0$  to  $\xi = \infty$ , as found by integration, is

$$V = \frac{V_0}{2(\pi kt)^{\frac{1}{2}}} \int_0^{\infty} e^{-\frac{(x+\xi)^2}{4kt}} d\xi = \frac{V_0}{\sqrt{\pi}} \int_{\frac{x}{2\sqrt{kt}}}^{\infty} e^{-\beta^2} d\beta$$

$$= \frac{V_0}{2} \left[ 1 - \frac{2}{\sqrt{\pi}} \int_0^{\frac{x}{2\sqrt{kt}}} e^{-\beta^2} d\beta \right] \dots\dots\dots (27)$$

We could arrive at the solution for this case by using Fourier's integrals, as we did for equation (23), giving  $f(x)$  the value  $V_0$  from  $x = -\infty$  to  $x = 0$  and the value zero from  $x = 0$  to  $x = \infty$ . We get at once equation (27) again.

This latter method gives the exact solution for the problem and yet it gives the same result as the former method, from which one might expect naturally enough an approximate solution, since we get it by integrating solutions that were approximate. This is the point to which attention was called in applying our results to this case; we have the integration of approximate solutions an exact solution. The first explanation offered of this unexpected result is apt to be that the approximation used is the more exact as the distance  $x + \xi$  is the greater; but we have seen earlier that just the contrary is true and that at great distances (20) ceases to be properly called a solution unless the time is taken very great. The real explanation is simply that the operations of summation and integration are not always the same, and this is a case in point. Nothing is commoner in applying mathematics to physics than to use mathematical processes with laxity and to test the legitimacy of the application by the results. It is so uncommon to have a summation made improperly by integration that we lose sight of the mathematical fact that the operations are not equivalent. We take similarly the first two terms of a Taylor's series expansion as a sufficiently close approximation in almost any piece of analysis, without questioning whether the function under consideration can be so expanded and without reference to the value of the terms disregarded; we take differential coefficients without asking whether they can have a meaning, etc. The good excuse offered is that the chances are overwhelmingly in our favor, and that if we have made a mistake we shall quickly find it out from the results. Had we actually made a summation in the above problem we should have got an approximate result, but by integrating we get the limit toward which the summation tends as  $d\xi$  tends towards zero, and it happens in this case that this is the exact solution. In finding an area we take a series of strips of area of  $y dx$  and however infinitely small  $dx$  is, so long as it is something and not zero, the sum

of such strips is not the exact area required;  $\int y dx$  is the limit toward which the sum tends as  $dx$  tends to zero, and we know from the familiar example of Fourier's series how the value can change actually in the limit. It happens in the present case that as  $d\xi$  is made smaller and smaller, and  $V_0$  correspondingly greater and greater in order to keep  $\sigma$  constant, in the limit  $\frac{\sigma}{2(\pi kt)^{\frac{1}{2}}} e^{-\frac{x^2}{4kt}}$  is the exact solution for an infinite plane (see under (21) and (22)). So in making the integration above, that is, in finding the limit of the summation, we get necessarily an exact solution because in the limit each term of the solution is exact. Had we approached the limit in some other way than in keeping  $\sigma$  constant we might have got quite a different result.

The forms of the curves for (27) are shown on Plates XXVII and XXVIII. Curves  $E^1, E^2$  and  $E^3$  are drawn with values of  $x$  as abscissæ for values of the time  $\frac{1}{16k}, \frac{1}{4k}$  and  $\frac{1}{k}$  respectively; curves  $F^1, F^2$  and  $F^3$  are drawn with values of  $4kt$  as abscissæ for values of the distance  $\frac{1}{4}, \frac{1}{2}$ , and 1 respectively.

Since the current or flow is got from the temperature by a differentiation with regard to  $x$ , and since equation (27) was got from (20) by an integration with regard to  $x$ , it is evident that the curves for the potential or temperature in (20) are the curves for current in the present problem.

$$I = -K \frac{\partial V}{\partial x} = \frac{K I_0}{2(\pi kt)^{\frac{1}{2}}} e^{-\frac{x^2}{4kt}} \dots\dots\dots (28)$$

These curves are given on Plates XXIII and XXIV for points to the right of the origin; the form for points to the left is obvious, since the curves are symmetrical about the  $y^z$  plane.

PHYSICAL LABORATORY, BRYN MAWR COLLEGE.

April 3, 1902.

## A NEW METHOD OF TRANSITING STARS.

BY MONROE B. SNYDER.

(Read April 4, 1902.)

The method of observing transits of stars, here to be described in a preliminary and general manner, consists in driving the micrometer screw and hence micrometer thread of a transit instrument by means of an electric motor at the uniform speed pertaining to any given declination, at the same time that the observer by secondary adjustment secures and maintains accurate bisection of the star, while given positions of the screw and hence thread are automatically recorded on a chronograph.

It is now more than four years since the writer described the method to his associates interested in astronomical observation. In the autumn of 1899 this plan of electrically driving the transit thread was also mentioned to Professors Wadsworth and Morley and at some length discussed with the latter. Working drawings of the special instrument which at present gives concrete expression to the method were completed in September, 1900. The "electrical transiter," or more simply "transiter," as for brevity the new device has been named, was mounted on the small meridian circle of the Philadelphia Observatory in February, 1901, and there subjected to many tests and improvements since. The demands on the writer's time have, however, not permitted that singleness of devotion which the transiter and its interesting method should receive, and it does not, therefore, seem desirable any longer to withhold a preliminary communication on the subject.

The fundamental idea of moving a transit micrometer wire by means of clockwork synchronously with the star's motion was proposed in 1865 by Braun.<sup>1</sup> But to Repsold is due the persistent pursuit of the idea that personal equation can be banished from transit observations by mechanical methods. And although his practical solutions of the problem have hardly proved adequate, they have stimulated and permitted serious efforts on the part of observers.

The first suggestion of Repsold,<sup>2</sup> made in 1888, was to mount the

<sup>1</sup> Dr. Carl Braun, *Das Passagen-Mikrometer*, Leipzig, 1865.

<sup>2</sup> F. Repsold, "Durchgangs-Instrument mit Uhrbewegung," *Astron. Nach.*, 2828.

base of the transit instrument on a polar axis and within a limited range drive the instrument to the diurnal motion by means of clockwork, and in some undescribed manner keep the star bisected so as to determine the meridian passage through electrical signals automatically made. The plan admirably met the chief difficulty of the varying rate of motion due to difference of declination, but was abandoned on account of the great mass to be moved.

It has to the writer, however, seemed likely that by applying a powerful electric motor of strictly constant speed, and by using a second electric motor with regulable speed for driving one element of a differential gear which engages the shaft driven by the main motor, or by several other electrical devices not requiring mention, an equatorially mounted transit instrument can be driven to stellar bisection and readily kept so adjusted.

A second plan, "Neuer Vorschlag zur Vermeidung des persönlichen Zeit-Fehlers bei Durchgangs-Beobachtungen," was proposed by Repsold<sup>1</sup> in 1889 and tested by Becker<sup>2</sup> in 1891 with moderately favorable result. A new form of micrometer, made for the Madison Observatory by Repsold,<sup>3</sup> was described in 1896, and with the general plan of its construction the writer became acquainted in the autumn of 1897. This specially designed and rather complicated micrometer requires that star bisection shall be maintained by twirling the micrometer shaft alternately with each hand of the observer. While this twirling is proceeding the ten electrical contacts of a drum mounted on the micrometer screw determine as many records on the chronograph. This Repsold method, while not lacking in ingenuity, seemed to the writer to labor under the following defects: An alternating twirling motion of the micrometer, even when communicated with the greatest adroitness, is not approximately a uniform motion. The observer is attached to the instrument by both hands, and is incessantly committed to the most painful attention. Good results could hardly be secured without the most prolonged and painstaking practice. Through his special habit of twirling each observer must have a new form of

<sup>1</sup> F. Repsold, *Astron. Nach.*, 2940, 1889, September.

<sup>2</sup> Prof. E. Becker, "Ueber einige Versuche von Durchgangs Beobachtungen nach dem neuen Repsold'schen Verfahren," *Astron. Nach.*, 3036, 1891, März.

<sup>3</sup> "Neue Mikrometer von A. Repsold u. Sohne," *Astron. Nach.*, 3377, 1896, Juli.]

personal equation. Even the averaging secured by the great number of electrical contacts does not certainly eliminate the peculiarities of a given habit of twirling. At any rate the great number of signals to be read from the chronographic sheet constitutes a very serious infliction on time and patience. Finally, the Repsold method does not, during any given star transit, offer a ready and direct means of comparison with the ordinary methods of observation.

The difficulties experienced in acquiring reliable observing habits with the Repsold transit micrometer are evident from the reports of Becker,<sup>1</sup> Kowalski,<sup>2</sup> and Flint.<sup>3</sup> The latter is, it seems, the only American observer who has tried the Repsold device to any extent, and he says that "after considerable practice" he obtained the same probable error by the method for "a signal under good conditions as for a single thread when observing with a fixed reticule and chronograph."

And yet it is not surprising that among European observers engaged in longitude work, the Repsold method should after prolonged discipline yield excellent results. Albrecht,<sup>4</sup> in an extended paper on its application to longitude work, points with enthusiasm to the superior results obtained. He considers the former indifferent results to be due to lack of practice and insists that the highest effectiveness, by this method, is attained only after a long season of active experience. "Man erlangt das Maximum der Leistungsfähigkeit doch auch bei dieser Methode erst nach langer Uebungszeit."

These experiences of practiced observers, while pointing to the value of the plan of micrometer thread motion in eliminating personal equation and its variations, confirm the anticipations of the writer as to the inherent defects of the Repsold method. It is therefore interesting to note that experiments for relieving some of the imperfections of the method have been going on at the Konis-

<sup>1</sup> *Loc cit.*

<sup>2</sup> *Ueber das neue selbstregistrirende Mikrometer von Repsold*, Petersburg, 1897.

<sup>3</sup> Albert S. Flint, "The Repsold Micrometer of the Washburn Observatory," *Astron. Jour.*, No. 470, 1899, September.

<sup>4</sup> Prof. Th. Albrecht, "Die Beobachtungsmethode mittelst des Repsold'schen Registrirmikrometers in ihrer Anwendung auf Längenbestimmungen," *Astron. Nach.*, 3699, 1901, März.

berg Observatory, where its Director, H. Struve,<sup>1</sup> has successfully applied clockwork directly to the Repsold micrometer, and thus unquestionably improved its usefulness. With this work the writer became acquainted only after his own plan had been consummated and the resulting instrument constructed and mounted for use. Dr. Cohn,<sup>2</sup> of the same Observatory, has recently published an extended investigation which shows marked advances in accuracy over the usual methods of observing. Struve's method has, however, thus far involved the unsymmetrical placing of the weight of the apparatus and, while itself possessing serious mechanical limitations, does not avoid certain peculiarities and limitations of the Repsold micrometer. The necessity therefore still exists for a method that shall be flexible in adaptation and use, and not impose unreasonable conditions on the observer.

The conditions to be attained in an effective method were early formulated by the writer substantially as follows:

The ordinary micrometer of a transit instrument shall be used, and its movable wire driven electrically at approximately uniform speed. The rate of driving shall, as required, vary with the declination. The direction of motion shall be instantly reversible. The wire shall be promptly readily started on its course when bisection of the star occurs. While in motion the wire shall be easily regulable for bisection of the star. The automatic chronographic record shall be made at whole turns or at fractions of a turn of the screw as desired.

In practically studying the electrical method of determining and controlling the motion of the thread of a transit micrometer, it has been found that there are three principal plans of adaptation available:

I. A small electric motor may be placed on or near the head of the transit instrument, with its axis parallel to that of the instrument. The varying rate of motion required for change in declination may then be secured by regulating the field of the motor and, if necessary, also that of a small dynamo supplying the current. The main difficulties in this plan are, the wide range of

<sup>1</sup> H. Struve, "Ueber die Verbindung eines Uhrwerks mit dem unpersönlichen Mikrometer von Repsold," *Astron. Nach.*, 3719, 1901, März.

<sup>2</sup> Dr. Fritz Cohn, "Ergebnisse von Beobachtungen am Repsold'schen Registrirmikrometer bei Anwendung eines Uhrwerks," *Astron. Nach.*, 3766-67, 1901, November.



speed regulation required and the interference due to inertia at starting.

II. Equatorial speed that is absolutely constant but slightly regulable may be given the motor, similarly placed, and the differing rate of motion proper to each declination determined by mechanical gearing, consisting principally of two friction disks placed at right angles to each other, or by some other mechanical equivalent. Both of these plans require special care in the construction and mounting of the motor, so as to obviate the communication of injurious vibration to the transit instrument.

III. It may in some instances be desirable to place the electric motor on a separate support near the base of the instrument, and then by means of a light steel shaft entering the axis of the transit finally communicate the required motion to the micrometer screw. All the motions and controls peculiar to either of the other plans may be secured to this form of transiter, excepting that the micrometer cannot at all be driven during the time necessary for reversal of the transit instrument. This limitation would in some instances be rather annoying, if not destructive of facilities the method should furnish.

It is also quite feasible to place certain elements of the transiter on a separate support and communicate the motion to a small slow-speed alternating current-motor placed on the head of the transit instrument and connected with the micrometer, and so obviate practically all the mechanical and electrical difficulties. Experiments in this direction are in progress.

In the attempt made to actualize the electrical method of driving the transit micrometer contending obstacles and facilities led, for a first trial, to the selection of the second plan mentioned, namely, that of gearing from a small motor of fixed speed placed near the head of the instrument. In reaching this conclusion the writer was greatly assisted by his friend and former student, Dr. H. G. Geissinger, who, immediately the method of the electrical transiter and the conditions it imposed had been described, became enamored of the delicate mechanical and electrical problem. Detail drawings of a transiter of this type were prepared under the writer's direction by Dr. Geissinger, and he has introduced several ingenious devices which admirably meet the conditions set. The special aim of the writer is to construct a form of transiter that may, without serious modification, be attached to any transit instrument. It should not involve a special form of micrometer nor in any way vitiate the in-

strument for its usual work however accurate. Excepting in the unnecessary weight of the parts and general coarseness of the mechanism, the transiter as now constructed fairly meets all the demands originally set and besides introduces some new conveniences. Although it is not the intention at present to give a detailed description of the transiter, it may be allowable briefly to mention several of its advantages:

Regulation of the bisection of a star is easy and definite. A record is made but once for each revolution of the micrometer, and records will be increased in frequency only as special work demands. A predetermined schedule of recording can be determined for any given run of the micrometer. Back lash of the screw on reversal of motion may be completely eliminated by the adjustment of the electrical contacts. The whole transiter may be balanced symmetrically on the instrument, and thus changes in the instrumental constants avoided. Instantaneous reversal of the motion of the micrometer permits of many conveniences as to method of work. In determinations of time and longitude the tendency has of late been to reverse the transit instrument during the passage of each star, and thus to eliminate a series of errors and facilitate reductions. The transiter by its ability to reverse motion instantly, and even automatically, lends itself readily to this method of work.

From the beginning of 1901, when it was completed, until the present the transiter has been the subject of many tests and of some improvements, and for a year or more it is hoped it may be destined to progressive change. It is now mounted on the four-inch meridian circle, for which it is expected a suitable place may be found at the Suburban Photographic Station of the Observatory, when this Station shall have been definitely located, but only after the completion of the present series of experiments with the transiter, and the determination of the latitude and longitude of the City Station of the Observatory.

Personal equation in all its variations remains a much more serious factor than many painstaking astronomers, who have not sufficiently practiced their accuracy even against a simple personal equation machine, are willing to admit. It is then gratifying to find that Professor Langley<sup>1</sup> has recently been willing to propose

<sup>1</sup> Prof. S. P. Langley presided at the meeting, and had at a recent meeting of the American Astronomical and Astrophysical Society described his new and very ingenious method of obviating personal equation in any time observation.

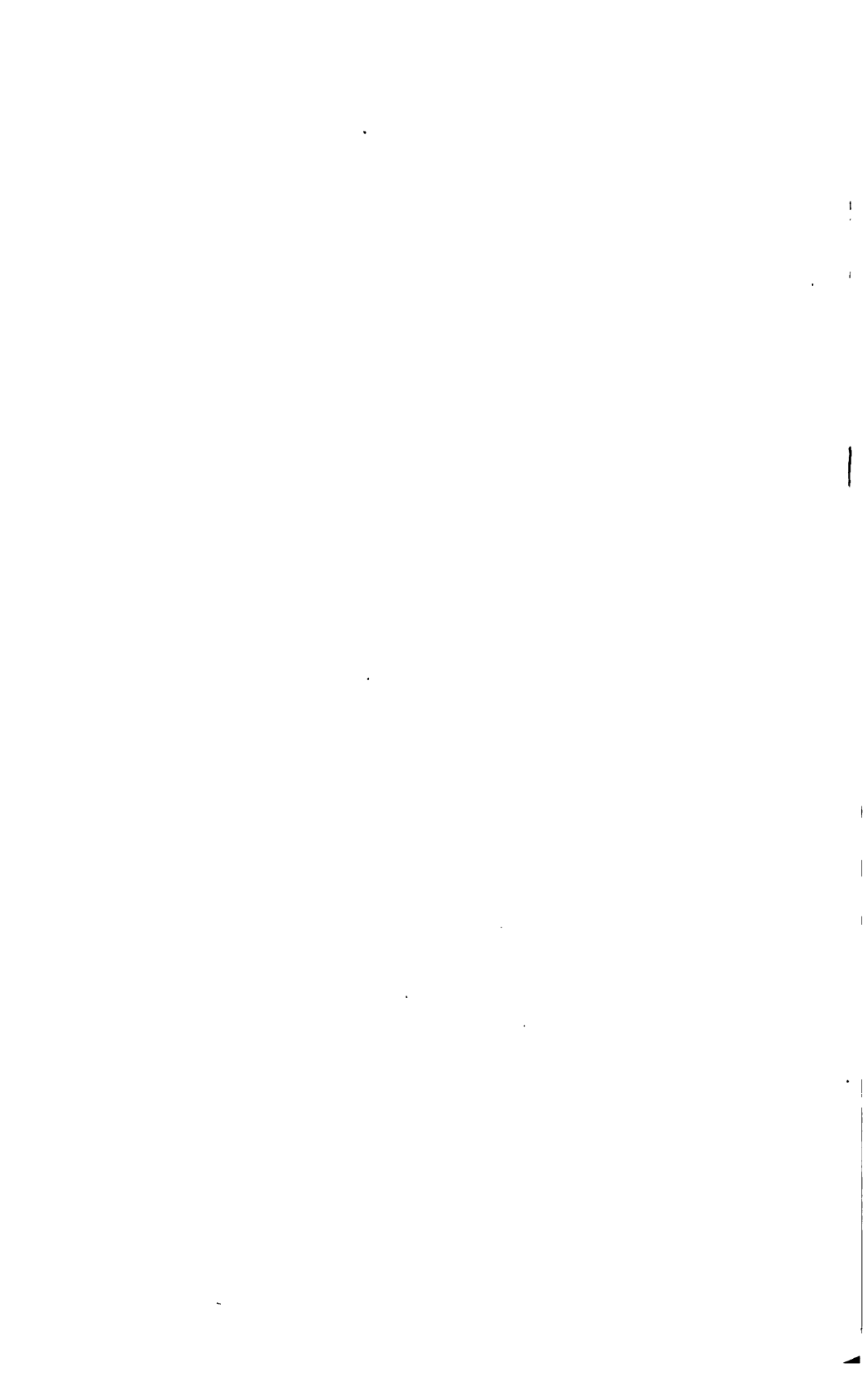
an entirely novel and highly suggestive method for its elimination in many classes of observation. And it may therefore be permissible, in this presence, to draw attention to the fact that the method of the electrical transiter permits for the first time the determination of the absolute personal equation at any and every desired star transit, and on the star itself. While reserving a complete discussion of this subject for a future occasion, it should be stated that several plans offer themselves to this end in the transiter. To mention but one: The usual wires are undisturbed, and the transiter can be adjusted so as to cut itself in and out automatically at certain parts of the run and only there receive the attention of the observer for star-bisection. At other portions of the run the usual method of chronographic signals, or even of the eye and ear method may be employed, and so, on reduction to the middle, be compared with the transiter's automatic signals. Personal equation may thus be studied with facility on the stars themselves and its variability traced through a simple observation or a series of observations, and whatever is sufficiently stable expressed as a function either of the stellar declination or of stellar magnitude or even of the physical condition of the observer.

It seems rather likely that finally all such study of the personal equation, when it shall have clearly demonstrated the unreliable character of the usual methods of transit observation and the adequate accuracy of the newer method, will be relegated to the Psychological Laboratory. Certain it is that the banishment of reaction time from transit observations and the reduction of this class of errors to those of bisection, either of a star image by a thread or of a thread interval by a star, means an epoch in observational astronomy whose actual realization by suitable devices is a worthy challenge to our best efforts.

With an automatic transiter allowing easy and accurate bisections, a chronograph recording with the utmost accuracy, and a clock of the best mechanism kept under constant pressure and temperature, a new field for accurate work in longitude determination and in the evaluation of stellar position and stellar parallax would be opened to the activity of the astronomer.

PHILADELPHIA OBSERVATORY, March, 1902.





PROCEEDINGS  
OF THE  
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A CRETACEOUS AND LOWER TERTIARY SECTION  
IN SOUTH CENTRAL MONTANA.

(Plate XXIX.)

BY EARL DOUGLASS.

*(Read April 3, 1902.)*

This paper is intended only as a preliminary report of an interesting geological section—an account of what has been done and a suggestion of what is yet to be accomplished. The points of interest are: (1) The completeness of the Upper Cretaceous which overlies the older beds, probably Jurassic and Lower Cretaceous, and underlies the Fort Union, which here contains mammalian remains, correlating it with the Torrejon of New Mexico; (2) the excellent exposures of the strata, giving a good opportunity for study; and (3) the occurrence of interesting fossils, especially vertebrates, in several different horizons.

The region here referred to lies east of the Crazy Mountains and south of the Big Snowies, in the basin of the Musselshell River, in Sweetgrass County. It extends from south of the Musselshell River southward twelve or fifteen miles, and eastward from a line passing southward from Harlowton on the Musselshell about the same distance. This is part of the south limb of a broad anticline, the general trend of which is south of east. This anticline is dissected longitudinally by the Musselshell. The lowest strata exposed are upheaved into a dome-shaped uplift southeast of Harlowton and four or five miles south of the river, where strata which are apparently of Jurassic age are exposed.

This region is on the western border of the elevated plains country, and occupies a position intermediate between the plains and

the foothills. The strata are, as a rule, not horizontal, but have been affected by the disturbances which have elevated the mountains farther to the west or north. In restricted localities the beds are horizontal and in others nearly vertical, and there are all intermediate grades. The average dip is probably not more than fifteen or twenty degrees.

The relief beautifully expresses the geological character. Through the whole section there are alternations of sandstones and shales and all grades between the two. Sometimes, as in the Fort Benton and Fort Pierre, the shales predominate and attain a considerable thickness. Again, as in the Dakota (?), Niobrara, Fox Hills, etc., sandstones predominate—at least there is enough indurated sandstone to retard erosion and to produce prominent ridges which can be followed for long distances—fifty miles or more. In all the formations there is considerable sandstone, and in all there is much shale; but I have seen but very little limestone in the whole section, though it sometimes occurs in concretions or in thin layers.

It does not appear that during the whole period of deposition the sea ever attained any great depth. Probably it was deepest at times during the Benton epoch, yet even here the great amount of sand in the shales indicates near-shore deposition. The erosion features will be given in the descriptions of the different formations.

So far as I am aware this particular region has been described only by the writer (see *Science*, January 3, 1902, p. 31, and February 14, 1902, p. 272). A little to the west is the area mapped in the Little Belt Folio (No. 56) of the U. S. Geol. Survey, and some work was done to the eastward on Swimming Woman and Careless Creeks by W. Lindgren and George H. Eldrege, in connection with the Northern Transcontinental Survey.<sup>1</sup>

Of course there is no single section where all the features here described can be seen, and the depressions or ridges into which the different strata weather have frequently to be followed for a few miles to obtain good exposures. Fortunately this is easily done.

The Lake Basin, to which reference will frequently be made, is a large, depressed area nearly fifty miles long east and west and twenty-five miles north and south in the widest portion. The former represents the greatest east and west extension. The eastern portion extends northeastward. This portion I have not ex-

<sup>1</sup> *Tenth Census of the United States*, Vol. XV, p. 243.

pled. The basin has no outward drainage, but has several small lakes without outlets, into which small streams empty, when there is an excess of precipitation. The basin is bounded on the south by the high rocky bluffs of the Fox Hills, and on the north, at least in the western portion, by the hard sandstones of the Niobrara and the Dakota (?). The name Lake Basin seems doubly appropriate, for it not only contains lakes, but it resembles the bed of some ancient body of water with bays and inlets, and with capes, promontories and peninsulas extending into it from the southward. The scene is spread out like a great panorama; the southern hills and northern ridges become hazy in the distance and the farther border seems a dim ridge on the eastern horizon. At the foot of the Fox Hills bluffs are the Fort Pierre shales and still farther away the Fish Creek beds.

As the principal object of this paper is to show something of the characters of the uppermost Cretaceous and Lower Tertiary formations in this locality, and to give a little light tending toward the clearing up of the problem concerning the boundary between the Mesozoic and the Cenozoic ages in the Rocky Mountains, I will give only a brief sketch of the formations lower than the Niobrara.

#### JURASSIC, ETC.

The supposed Jurassic is exposed in a dome-shaped uplift, so that the strike of the outcrop is nearly a circle. The beds are sandstones and sandy clays. The latter are largely red in color. This is apparently due to the combustion of coal. There are bones of large *Dinosaurs* and of some smaller reptiles, but they have not been studied. It is possible that this stratum with the sandstones above may belong to the Lower Cretaceous. There are many hundreds of feet of hard sandstones and shales between the fossil-bearing horizon and the Fort Benton. The upper portion probably belongs to the Dakota formation.

#### *The Fort Benton Formation.*

These beds and their contained fossils are much like the corresponding ones in other regions. They are principally dark shales with bands of sandstone in the lower portion, and in one place I found a half dozen specimens of *Prionocyclus* Meek in brown concretions in the shales. Higher were *Ammonites*, *Scaphites*, *Inoce-*



*rami*, small *Baculites* and other *Mollusca*, all of Benton types. These shales weather into ravines between the sandstones of the Dakota below and the Niobrara above.

### *Niobrara.*

In the Niobrara gray sandstones predominate, though there are beds of shale. This differs from the usual character of this formation in most other regions where it has been observed. It has usually been described as being composed principally of limestone and marl, though sometimes containing considerable sand. The sandstones here are very much like some of those of the Laramie, and near the middle portion are seams of coal. In two or three places I looked in vain for any well-preserved plant remains in the carbonaceous shales and in the sandstones above and below the coal, and followed ravines cutting through the prominent sandstone ridges without finding any good fossils. However, about twenty miles to the southeastward a few plant impressions were found—the best of which was apparently a *Sequoia*—in beds which I take to be Niobrara. Undoubtedly, by careful, continued search, a fair collection could be obtained.

In one place, where Mud Creek cuts through the formation, the beds approach near to a vertical position. I should not estimate the thickness to be less than 700 or 800 feet here. It may be more. The sandstones form a prominent ridge where they are much inclined. These ridges are sometimes wooded, though the trees are usually not very large or numerous.

### *Fish Creek Beds.*

Above the Niobrara are beds which I believe to belong to the Belly River formation, but until they are certainly correlated with the latter I give them the above name.

They are best exposed between Fish Creek and Mud Creek, only a few miles from where the latter empties into the Musselshell River. Here they are nearly horizontal, while the underlying Niobrara dips at a considerable angle to the southward. Farther to the east and west I did not notice any unconformity between the two formations. In the above-mentioned locality, where they are horizontal, they weather into "bad land" forms. The material is principally rather soft sandy clay, with hard, almost black concre-

tions and hard sandstone layers. In the latter there are, in some places, plant impressions. The softer layers contain fossil wood, bivalve mollusks, turtles and bones of *Dinosaurs* of the genus *Claosaurus*. The bones are generally petrified and occur also in the dark concretions which also contain plant remains. Though they are, as a rule, excellently preserved, yet sometimes there is what seems to be a good portion of a Dinosaur broken into myriads of little fragments. The beds are probably either fresh or brackish water.

This formation was observed in several places in this region, and in all there were bone fragments; but we found no other equally good exposures. About twenty-five miles to the southeast, in the Lake Basin north of Columbus, the formation lying immediately below the Fort Pierre in one place has a considerable thickness of sandstone containing petrified logs, but only one or two small fragments of bone were found. Some of the plants of this formation are related to *Sequoia*. The bivalve shells were so fragile as to crumble with the soft matrix in which they were imbedded.

Lying over these beds is a series of shales and hard laminated sandstones. Some fossil leaves were seen in the latter. A series of dark shales, perhaps thirty feet thick, was carefully examined. The shales were full of carbonaceous plant fragments, and some fairly good leaves were found in the thin interbedded layers of sand or sandy concretions. I do not know whether these beds should be put in this series or in the Fort Pierre. I think it better to consider them, until they are more thoroughly explored, as belonging to the Fish Creek series.

### *Fort Pierre.*

Above the beds just described are the Fort Pierre shales. This represents a well-distinguished horizon, so well marked by lithological characters and by characteristic fossils that its position is beyond doubt. The description of the Pierre in Colorado, Wyoming, etc., would answer almost equally well for the formation here. Dark, soft shales predominate. There are occasional thin bands of sand and many brownish concretions which break into angular fragments. These sometimes contain marine fossils and sometimes a network of calcite seams. The best preserved invertebrate fossils are in these concretions. The shells are those of *Ammonites*, *Baculites*, *Scaphites*, *Nautili*, and small *Gasteropods* and *Cephalopods*.

Some hard limestone concretions are crowded with these small molluscs.

What distinguishes the Pierre here from that in other places is the presence of many vertebrate fossils. Several *Mosasaurs* have been found. In the summer of 1900, Mr. Albert Silberling and I found portions of two individuals, including a skull. In the summer of 1901, the Princeton Expedition in charge of Dr. M. S. Farr procured a nearly complete skeleton except the skull.

But the most interesting fossil remains are those of the *Dinosaurs*. They have been found to be more numerous here than the *Mosasaurs*. The greater number of them belong to the genus *Claosaurus* and apparently to described species. Two portions of skeletons belong to quadrupedal type, probably to the *Ceratopsidae*. A *Claosaurus* skull and the greater part of the skeleton was obtained for the Princeton Museum last summer (1901). The digging was easy, but the removal of the bones was slow and tedious, as they had to be hardened. Nodules had formed around some of them, but many were in clear shale. The skeleton was just above a layer of yellowish, partly consolidated sandstone two or three inches in thickness. There were some thin layers or lenses in the shale, in which the remains were imbedded. There was also a minute seam of coal not thicker than cardboard. Cones or ends of twigs of what appeared to be *Sequoia*, Ammonites, Scaphites, Baculites and other molluscs, and shark's teeth were found in the matrix while removing the skeleton. Only the teeth and a few of the shells could be preserved, as the fossils in the shale disintegrated on exposure to the sun and rain. The deeper into the shale excavation was made, the larger the flakes into which it would break. Quite a number of other portions of skeletons were found during this and the previous year. Often the bones are solid, though lying among the grass roots, where the soil is composed of the disintegrated shales. Sometimes the nodules surrounding the bones are very hard and flinty.

The finding of *Dinosaur* remains in these marine beds was unexpected, but the sea was evidently shallow. In some places there is much gypsum in good-sized crystals, or in minute ones scattered through the shales.

The Pierre beds being soft, have weathered into depressions. They are usually covered, except in restricted portions, with a good growth of grass, but are treeless except for a few small willows or

cottonwoods that occasionally grow along the streams. They make grass-clad rolling prairies, with small ravines cutting into the soft shales.

The transition beds between the Fort Pierre and Fox Hills are usually obscured by the material washed down from the bluffs of the latter; but on the ranch of Mr. B. Forsythe, near the head of a branch of Big Coulee Creek, they can be nicely seen. The shales gradually become more sandy, and contain bands of sandstone until the latter predominates and the shales become shaly sandstones or sandy clays. In them I found no trace of fossils.

### *Fox Hills.*

In this formation the hard sandstones form a prominent ridge adjoining the depression made by the Pierre. It is the next prominent ridge above the Niobrara. I have followed its base for about thirty-five or forty miles. In only one place was there any confusion or any difficulty in tracing it, and this was caused by some change in the geological structure obscuring the Pierre shales. The outcrop extends southeast and northwest. It forms the southern rim of the Lake Basin. It furnishes many springs which, uniting their waters, produce little streams that cut through the rocky ridge and flow out upon the Pierre flats. In the Fish Creek region they empty into Fish Creek. In the Lake Basin, if the water does not soak into the ground, they flow into the land-locked lakes. Where the streams form little cañons and ravines through the Fox Hills strata, they are fringed with trees and shrubbery. In little valleys and amphitheatres there are often springs surrounded by groves, which are very picturesque, and in the heat of summer these places form a delightful retreat from the almost treeless wastes around. The trees, which are principally evergreens, cottonwoods, poplars and willows, follow the streams a little way toward the Pierre flats and then disappear.

Though these beds usually appear to be sandstone ridges, yet in places where conditions of weathering are favorable they are seen to contain much sandy clay, and in places for a short distance resemble "bad land" forms.

Fossil leaves and reptilian bone fragments were found in considerable abundance. Dr. Farr brought back some of the fossil leaves, but they have not yet been determined. Most of the bones are too fragmentary to be of much use. Some teeth were recognized as

belonging to *Claosaurus*. The only fossil plant we were able to recognize in the field was a species of *Salisburya*.

Though this is probably still below the Laramie—at least there are thousands of feet of what is apparently Laramie above it—yet this is the highest level in which we found *Dinosaur* remains in this region. This is interesting, as in other regions the *Claosaurs*, with one exception, have come from beds which have been supposed to be above the Fox Hills.

It is not certain just where the Fox Hills ends and the Laramie begins. It is possible that these bones, or at least some of them, are in the lowest Laramie; but as the two formations represent differences in conditions of depositions rather than difference in age, as distinguished by change or progression of the fauna or flora, it is not so essential, except as bearing on the more interesting question of the extinction of a very remarkable class of animals and the occupation of their territory by a class that had for millions of years held a subordinate position.

Above the Pierre, in the Fish Creek region, are alternations of dark shales and gray sandstones. In places the sandstone is warped, twisted or made up of imperfectly concentric layers. Above these are brownish laminated and greenish or brownish unlaminated sandstones and sandy clays. Provisionally, I place the base of the Laramie above these latter beds. They contain fossil leaves and bone fragments.

### *Laramie.*

The lowest beds, which are here taken to be Laramie, are a series of alternating various-colored shales and gray unlaminated sandstones. There are several hundreds of feet of these and no fossils were found in them. There are in some layers brownish concretions, some of which are large and composed of sandstone. These beds form a depression, but not so low as that of the Pierre shales.

Over these lies about an equal thickness of similar sandstones and gray shales. The former are harder and form a bench or ridge. There are several thin seams of coaly matter and the shales hold impressions of ferns and other delicate plants different from what we observed elsewhere.

Near or at the top of this series there are at least two layers containing non-marine fossils. In one of the fossils are principally *Gasteropods* and in the other bivalves—probably *Unio*. It

is said that this layer extends for twenty miles up Fish Creek, but I have not tried to trace it, so do not know whether it is continuous or not. It is also said that these fossils gave the Mussel-shell River its name. Here we may be quite sure that we are in the Laramie, for fresh or brackish water conditions prevail, but it probably extends between 1000 and 2000 feet below.

Still higher are shales forming a flat or depression, above which are conical hills or hog-backs—the remains of dissected ridges cut through by ravines and by streams which are fed by springs in the Fort Union sandstone above. These hills or ridges are capped with brownish, compact, laminated sandstone. No fossils were seen except fragments of wood in the shale.

Above these sandstones dark shales again predominate. I cannot tell, at least without more careful study and observation, where the Laramie terminates and the Fort Union begins. In fact, it looks as if there were in this section almost continuous deposition from the Jurassic up. We found here no traces of the volcanic material of the Livingston formation, which only thirty or forty miles to the southwest is so well developed. It appears that here deposition went on quietly and uninterruptedly. There is little doubt that part of the strata were deposited synchronously with those of the Livingston. Here, so far as we have discovered, as in other places, Nature has left no waymarks and laid down no boundary line to distinguish between the great "Age of Reptiles" and the "Age of Mammals." There appears to be no sign of the disturbance that is supposed to have closed the Mesozoic and brought in a new order of things; yet only a few miles away there was a region of upheaval and of intense volcanic activity. The strata in the section under consideration have been disturbed, but the Tertiary beds are also involved in the upheaval. Perhaps microscopic or chemical examination may reveal the presence of fine volcanic material here.

Mr. W. Lindgren made three different measurements of the Laramie to the eastward of this region (see *Tenth Census of the United States*, Vol. XV, p. 744). In none of these does he make the thickness of the Lower Laramie to be less than 7000 feet. I do not think that this, as C. A. White<sup>1</sup> thinks probable, includes the Belly River, or anything lower than Fort Pierre. Lindgren's Upper Laramie, or Bull Mountain series, is probably Tertiary—apparently

<sup>1</sup> "Correlation Paper, Cretaceous," *Bull. 84, U. S. Geol. Survey*, p. 174.

Fort Union. What is supposed to be Laramie in the present section is very thick, probably approximating that of Lindgren's measurements. But here, as everywhere else, the boundaries of the Laramie are uncertain. Here, however, we have it confined between certain limits. We have below a characteristic Fort Pierre fauna and above a characteristic Fort Union flora. Just how much of that which intervenes is Laramie is not known. I have no doubt that here deposition was going on at the same time as that of not only the Livingston, but also of the Arapahoe and Denver beds. Whether these beds will ultimately be assigned to the Upper Laramie, or included in a separate formation, depends upon the results of future careful investigation.

#### TERTIARY.

##### *Fort Union.*

The dark shales just mentioned continue upward, changing little in character; but brown concretions become numerous, then layers containing shells of bivalve Mollusca, then occasional layers of sandstone, and above these, often capping the bluffs, heavy gray sandstones, usually hard, sometimes laminated and sometimes massive. Above this I cannot speak definitely, but think that the Fort Union continues much higher. The strata from the top of the bluffs south of Fish Creek, which make a bench sloping toward Sweetgrass Creek in the direction of Melville, perhaps belong to higher members of this formation. The strata are not always continuous for great distances, but vary locally; yet a general description can be given that will apply fairly well to the beds examined. There are dark gray shales that in many places weather to thin, flaky particles on the surface. The wind blows away this light material and leaves bare depressions without vegetation. The sandstones are usually hard, sometimes massive or imperfectly bedded, and in some places break into great blocks, which tumble down the steep sides of the bluffs.

In the Fish Creek region these heavy sandstones, which lie above the soft shales, form a long line of rugged bluffs extending along the south side of the creek from the neighborhood of Porcupine Butte eastward for twenty-five or thirty miles; then it extends southeastward, probably forming the divide between the Sweetgrass on the southwest and the southern branches of Fish Creek and Big

Coulee Creek ; but I have not examined all of this territory. I examined hastily the beds on Sweetgrass Creek east and a little north of Big Timber, where I made a collection of fossil leaves. The remains of a turtle were also found in the shale.

The portion of the Fort Union described in this paper apparently represents the upper portion of the Crazy Mountain section, as given by Weed in the *American Geologist* of October, 1896.

Fossil plants, *Unios* and *Gasteropods*, are abundant and may occur in any part of the beds favorable for their preservation. Last summer (1901) determinable Mammalian remains were found. As is well known, the exact position of these beds has been a matter of some doubt and difference of opinion. They have usually been assigned to the Tertiary, though they have been placed as low as the Cretaceous and as high as the Miocene.

The bones and teeth of *Mammals* which were found<sup>1</sup> are not numerous, but are sufficient to show that the beds are of nearly the same age as the Torrejon of New Mexico. They are :

*Mioclanus acolytus* (Cope).

*Anisonchus* very near to *A. sectorius* Cope.

*Euprotogonia puericensis* (Cope).

*Pantolambda caviroctis* (?).

*Pantolambda* (?), a small species.

Some others are doubtful.

I felt very certain that these beds were Fort Union, but to settle the matter forever and leave no room for a shadow of doubt, a box of fossil leaves was sent to Mr. F. H. Knowlton, of the United States Geological Survey. Mr. Knowlton examined them at once and sent me a list, which I quote :

*Pterospermites cupanioides* (Newb.) Knowlton.

*Populus speciosa* Ward.

*Populus amblyrhyncha* Ward.

*Ulmus orbicularis* ? Ward.

*Vitis xantholithensis* Ward.

*Populus daphnozenoides* Ward.

*Populus arctica* ? Heer.

*Platanus aceroides* Göpp.

*Celastrus* sp.

*Grewia crenata* (Ung.) Heer.

<sup>1</sup> *Science*, February 14, 1902, pp. 272, 273.



*Viburnum asperum* ? Newb.

*Populus cuneata* Newb.

*Populus* sp.

*Platanus nobilis* Newb.

*Platanus basilobata* Ward.

*Viburnum* sp.

*Paliurus* sp.

*Grewiopsis viturnifolia* Ward.

*Populus* ? n. sp.

Mr. Knowlton says: "The species are all Fort Union beyond a doubt."

Of a few shells which I enclosed, he writes: "The shells I showed to Mr. Stanton, and he says that the two large ones are *Unio Couesi* White; and the other pretty near to *Unio Endlichi* White."

The *Mammals* were found in the shale. The collection of fossil leaves was made in the sandstone a little higher up, though there are concretions and layers of sandstone that contain leaves in the same beds as the Mammalian remains. A portion of the collection was obtained on Sweetgrass Creek north of east of Big Timber, in the locality mentioned above.

#### GENERAL OBSERVATIONS.

The problem of greatest interest connected with the study of this section is that relating to the transition from Mesozoic to Cenozoic times. Of course, if deposition had been continuous, or nearly so, and there were no great faunal or floral migrations, there could be no distinct boundary between the two. There is a great difference between the Cretaceous as a whole and the Tertiary as a whole, but where are we to draw the line? If there was a time of widespread or general upheaval throughout the western portion of the continent, or of the Rocky Mountain region, this might form a convenient division. Upheavals and great volcanic activity certainly occurred in restricted localities, but we cannot at present prove that such were general or that they did not occur in different places and at different times. If we could point to any time when the *Dinosaurs* ceased to be and the higher orders of *Mammals* took their places, then the matter would be easy; but heretofore most of the Cretaceous *Dinosaurs*, in fact nearly all of them, have been

supposed to come from the uppermost portion of the Cretaceous—the Laramie—but the other fossils found in these beds have not been of a character to settle the doubt concerning the horizon. There is no direct proof that the Dinosaurs died out before higher forms of Mammals became numerous. Though they have not yet, so far as I know, been found in the same beds, yet there seems good reason for believing that Dinosaurs were contemporaneous with Puerco Mammals. Were it not for the “*Ceratops fauna*” and the discovery of a few specimens in the eastern United States and one in Kansas, we should say that the Dinosaurs died out at the end of the Jurassic. It would seem that if anything had a chance of being preserved it would be the large, solid bones of these animals; yet there are miles of thickness of strata and thousands of square miles of exposure of Lower Cretaceous, Dakota and Colorado beds, and nothing, I believe, has been found to tell that these animals still lived in this great Cordilleran region, except the type of *Claosaurus agilis* from the Niobrara of Nebraska. This rock must represent many millions of years in which Dinosaurs lived, flourished and progressed. To our view they disappear in their glory, and after ages appear again in glory but transformed; again they suddenly disappear and we see them no more. The morning, midday and evening of their splendor is lost to us. Until the discovery of the beds described in this paper almost nothing was known of them in the Montana formation, at least the beds from which they had been collected had not been considered as belonging to that age. The point the writer wishes to make is this: It is extremely unsafe to say when and where these strange reptiles breathed their last, for the presence of fossils is certain evidence of the existence of life, but the lack of them is no evidence of its absence. Dinosaurs may have continued long in the Eocene, but conditions in the places where so many Mammalian remains have been found may not have been favorable for them.

I think we can hardly account for the general absence of Dinosaur remains in the Kootenai and Upper Cretaceous, below the Laramie, by the beds being in part marine. Much of the strata is evidently fresh or brackish water. We should hardly expect to find them in the Benton and Fort Pierre shales associated with large marine Mollusca, yet as previously stated *we do find them* in the latter. This proves that these animals lived near the sea or where they could float into it. Why don't we get them then in the many

thousands of feet of sandstone which, if marine, must be near-shore deposits? It is true that any day we may hear of their being found in some of these strata, and we may also hear of their being found in Eocene strata, if they have not been found there already.

As shown by this paper, the presence of *Claosaurida*, and probably of *Ceratopsida*, is far from showing that the beds in which they are found are as late as Laramie—I mean as the Laramie as it is understood. It is true that the Fort Pierre, and in some places the Fox Hills with it, represents an incursion of the sea, and that conditions of life were not greatly different during the time of the deposition of the Belly River beds from what they were in the Laramie.

At present the fossil plants, together with orographic movements and their results when they occur, are the only things we can use to distinguish these doubtful formations as the Laramie, Livingston, Denver, etc. The plants, on account of mixtures of the flora of different horizons in collecting, have not been available for use until the material has been carefully separated. As Mr. Knowlton has been doing this work, his forthcoming monograph on the Flora of the Laramie and Allied Formations will be looked for with interest.

There is not much doubt that the Livingston in Montana represents the upper portion of what has been called the Laramie in the plains region farther to the east. Both have Laramie strata below; both are overlaid by Fort Union beds. In Colorado it seems that the Arapahoe, and probably the Denver, or the greater part of it, sustains the same relation to Laramie. Mr. Knowlton says: "From these considerations it appears beyond question that the flora of the Livingston formation finds its nearest relationship with the Denver beds of Colorado."<sup>1</sup> If the Livingston and Denver are of the same age, as has for some time been suspected, then the Denver must be older than the Fort Union, and therefore older than the Torrejon. With its apparently Cretaceous Vertebrate fauna, we are not warranted at present in placing the Denver much higher than the Livingston. It may be in part contemporaneous with the Fort Union.

The Puerco should be nearly of the same age, as it lies between Laramie and Fort Union (Torrejon) strata.

Below is given a table which is intended to show the probable

<sup>1</sup> *Bull.* 105, *U. S. Geol. Survey*, p. 63.

relations in time of the formations under consideration concerning which there is doubt:

*Table Showing Probable Relations of the Laramie and Overlying Beds in Different Regions.*

	<i>Cretaceous.</i>			<i>Tertiary.</i>
	Laramie of King			
In Wyoming.....				
	Laramie			Fort Union
Plains of Montana.....				
	Laramie	Livingston		Fort Union
Crazy Mts., Montana.....				
	Laramie	Arapahoe	Denver	
Denver Basin.....				
	Laramie	Puerco		Torrejon
Puerco River, N. Mex. ....				

The names given are the ones by which the different divisions have been called. There does not seem to be much doubt that the Livingston, Denver, Puerco, etc., are contemporaneous with what in other places has been assigned to the upper portion of the Laramie. Whether all will be included in the Laramie later will depend on the results of further careful investigation. I have indicated the doubtful division between the Cretaceous and Tertiary by a dotted vertical line passing between the Livingston and Fort Union and between the Puerco and Torrejon, or approximately so, not claiming that the time division line between the two sets of strata would fall exactly in the same place. The horizontal parallel lines are intended to represent contemporaneity of deposition. Deposition in the Denver Basin was not continuous and the blank spaces indicate non-deposition. The broken or dotted lines indicate probable continuity.

#### REMARKS ON THE FOSSIL MAMMALS.

The mammals are represented by about a half dozen species. Five of these are represented by teeth. Almost any one of these

taken alone would strongly incline one to the belief that the formation containing them is contemporaneous with the Torrejon of New Mexico. This is made still stronger by nearly every specimen. There are a radius and ulna which are different from any found in New Mexico, so that they cannot be assigned to any genus with certainty, and there is a premolar much like that of *Pantolambda*, but indicating an animal much smaller than any species of that genus, to which, however, I refer it with doubt. The other four are congeneric if not conspecific with Torrejon forms.

*Mioclanus acolytus* (Cope). (Plate XXIX, Figs. 9 and 10.)

This is represented by a small portion of a mandible with a molar tooth which is almost unworn. The anterior cusps are connate at base and much higher than the posterior ones.

*Anisonchus* Cope. (Plate XXIX, Figs. 3-5.)

This is also represented by a portion of a mandible. There are two teeth, a fourth premolar and a first molar. They are of nearly equal length. In size and character the teeth are nearly like *A. sectorius* Cope. It may, however, be another species.

*Euprotogonia puercensis* (Cope). (Plate XXIX, Figs. 6-8.)

Represented by a third premolar and a second molar of the right side and a third molar of the left. The molars differ somewhat from the type. Matthew has carefully studied the many specimens in the American Museum collection and finds a wide range of variation in the teeth, but no constant characters that will serve to separate the various forms which Cope has named. Of the many specimens no two appear to be exactly alike. I have compared the present specimens with those in the above collection and find that they do not differ so much from some of the American Museum specimens, as the latter vary among themselves. What comes nearest to being a distinguishing character is the smallness of the hypocone as compared with the protocone, but this is at least *nearly* paralleled by some of the above-named specimens.

*Pantolambda* (?) (Plate XXIX, Figs. 1, 2, 14.)

There are the greater portions of a radius and ulna, and two phalanges which are different from anything described from the

Torreon. They more resemble in some respects the corresponding bones of *Coryphodon*.

The ulna is much larger than the radius, is broad antero-posteriorly but narrow transversely. The upper portion of the olecranon is broken off, but a cross section above the glenoid cavity is triangular with the anterior edge thin. The sigmoid cavity is convex transversely. The outer portion is much less convex longitudinally than the inner; it extends lower and its upper portion makes an oblique emargination on the outer side of the olecranon. There are two fairly large surfaces for articulation with the radius. The upper outer surface of the bone has a quite deep longitudinal furrow which dies out near the middle of the shaft. The inner surface is longitudinally concave from the olecranon to the enlargement near the distal end of the bone, where there is considerable swelling and roughening. The distal articular surface is elliptical, slightly concave palmo-dorsally and convex transversely. This surface is very slightly oblique to the long axis of the bone.

The radius is subcylindrical above. The head is partly broken, but the surface for articulation with the humerus is shallow and appears to have been nearly circular. There is a longitudinal roughening on the ulnar side, to correspond with similar rugosities on the radial side of the ulna. Below these is a rugosity on the antero-inner side of the radius and on the opposite side. The bone has the appearance of being twisted on itself. The form of the bone suggests freedom of motion of the limb other than a fore-and-aft movement.

A proximal and medial phalanx apparently do not differ greatly from those figured in Osborn's paper on "Evolution of the Amblypoda."<sup>1</sup>

	M.
Length of ulna from upper portion of glenoid cavity	.1970
Antero-posterior diameter at middle of shaft	.0310
Transverse diameter at middle of shaft	.0143
Transverse diameter of shaft of ulna at middle	.0195

*Pantolambda cavirictis* Cope (?).

Fragments of upper jaw, with teeth from which enamel has been removed. The size is nearly the same as the corresponding teeth

<sup>1</sup> *Bull. Amer. Mus. Nat. Hist.*, Vol. X, p. 187.

of *P. cavirictis*, and there is nothing to distinguish it from that species.

*Pantolambda* (?) sp. (Plate XXIX, Figs. 11-13.)

An upper premolar, much smaller than  $P^4$  of *P. bathmodon* or *P. cavirictis*, but it is possible that it may be a  $P^3$  of nearly as large a form. It is very doubtful, however, whether it belongs to *Pantolambda* at all. The protocone is more conical, the outer slope on the median line of the tooth is steeper and the inner less so. The outer surface near the base of the crown is more concave.

A canine found with the above is not like that of the known species of *Pantolambda*, but can hardly be distinguished from that of modern Carnivores. It probably belongs to some Creodont.

PRINCETON UNIVERSITY, May 24, 1902.

#### EXPLANATION OF PLATE XXIX.

FIGS. 1 and 2. Ulna and radius possibly belonging to some species of *Pantolambda*.  $\frac{2}{3}$  natural size.

FIGS. 3-5. *Anisonchus sectorius* (?)

Last lower premolar and first lower molar with portion of mandible. Outer and inner view of mandible and upper view of teeth.  $\times 2$ .

FIGS. 6-8. *Euprotogonia puericensis*.

6. Right upper second molar.  $\times 2$ .

7. Left upper third molar.  $\times 2$ .

8. Right third upper premolar.  $\times 2$ .

FIGS. 9, 10. *Mioclanus acolytus*.

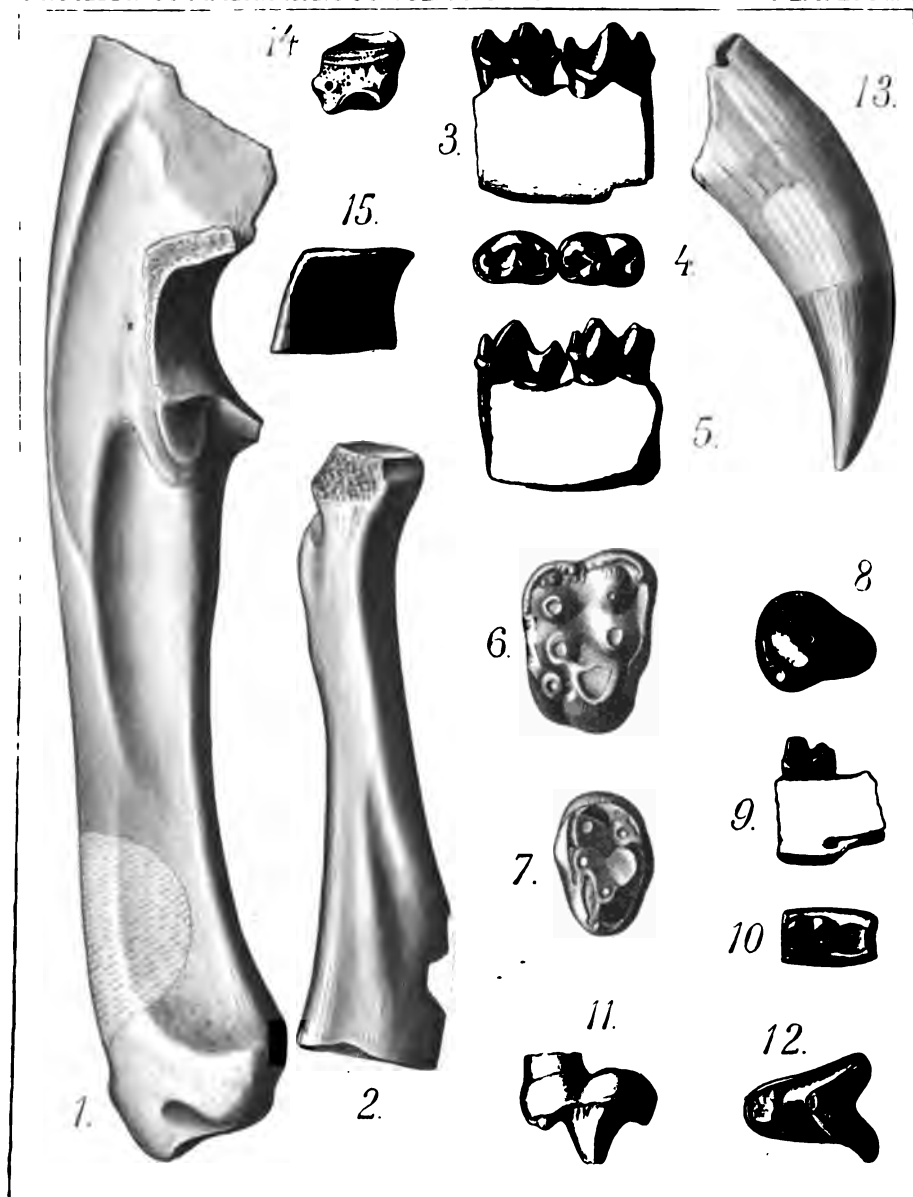
A lower molar with portion of a mandible.  $\times 2$ .

FIGS. 11-15. *Pantolambda* (?). Upper premolar.  $\times 2$ .

13. Canine tooth found with 11.

14. Phalanx found near 1 and 2.  $\times \frac{2}{3}$ .

15. Scale of *Lepidosteus* found with mammals.  $\times 2$ .



F. A. Peterson del.

FORT UNION MAMMALS.





## AREOGRAPHY.

BY PERCIVAL LOWELL.

*(Read April 4, 1902.)*

1. Facts familiar to the specialist are often credited with a general appreciation they do not possess. Immersed in his own line of research, the investigator forgets that others are not as intimate as he with some of the fundamental points of his inquiry, and omits as truisms what to others are not even known for truths. Areography is such a subject. Probably no one outside of the pursuit is aware how cogent is the conclusion to be derived from an inspection of the maps that have been made of the planet, as to the reality and the relation of the markings there depicted. Nor was it indeed till after I had compared these maps with some particularity that certain deductions from them forced themselves upon me. It will perhaps, therefore, not be unproductive of result if I present at this general meeting a collective view of the maps which have from time to time been made of Mars and note what they imply. Maps speak best for themselves, and with very slight introduction can be made to tell their own story better than any amount of text.

2. Of the maps here brought together, the earlier are taken from Flammarion's thesaurus *La Planète Mars*, Proctor's Dawes' map from his own book, Schiaparelli's from his memoirs in the *Accademia dei Lincei*, and the later ones from my own work. Of these latter, that for 1896-97 is the result of my own synthesis of the Flagstaff and Mexican observations of the Lowell Observatory for those years, while the ones for 1898-99 and 1900-01 I have but just completed, and they appear here for the first time.

3. All the maps here given marked in their day the point that areography had then reached. With but two exceptions, that of Flammarion and Proctor, therefore, they represent original observations made by the maker of the map himself or under his direction, and show in procession the evolutionary development of the subject. Such maps as failed to add to existing knowledge and are valuable merely as confirmatory documents have not been included. On the other hand, no map which materially contributed anything has been left out. Many excellent charts, therefore, have had to be omitted, not always because they presented nothing new, but

because contemporaneous ones included practically all their discoveries with additions. Of these, Cerulli's maps of 1896-97 and 1898-99 and Flammarion's of 1900-01 deserve special mention. The omitted maps confirm, not invalidate, the conclusions here drawn.

4. Twelve maps constitute the series. Of these the ordering chronologically runs thus:

I.	Map of Beer and Mädler . . . . .	1840
II.	Map of Kaiser . . . . .	1864
III.	Map of Dawes, by Proctor . . . . .	1867
IV.	Map résumé by Flammarion . . . . .	1876
V.	Map of Schiaparelli . . . . .	1877
VI.	Map of " . . . . .	1879
VII.	Map of " . . . . .	1881-82
VIII.	Map of " . . . . .	1883-84
IX.	Map of Lowell . . . . .	1894
X.	Map of " . . . . .	1896-97
XI.	Map of " . . . . .	1898-99
XII.	Map of " . . . . .	1900-01

Mercator's projection is used in all the maps. The zero meridian is in the same point on the planet in all except Kaiser's, though that meridian does not always fall on the same part of the plate, being in I, IX, X, XI and XII on the extreme left, in III, IV, V, VI, VII and VIII in the centre. Beer and Mädler's map is given by Flammarion on a stereographic projection which, for the sake of inclusion in the present series from its age and chronological importance, has been changed to Mercator's. All other circumpolar projections have been omitted.

5. It will be seen from inspection of the maps, and would be simply corroborated by further additions to the list, that increase in our knowledge of the surface of Mars falls naturally into four divisions or stages of development. The first of these is pre-cartographic; the second extends from 1840 to 1877; the third from 1877 to 1892; the fourth from 1892 to the present day. The first three of these divisions correspond to those given in Flammarion's *La Planète Mars*. The fourth is since the publication of that book.

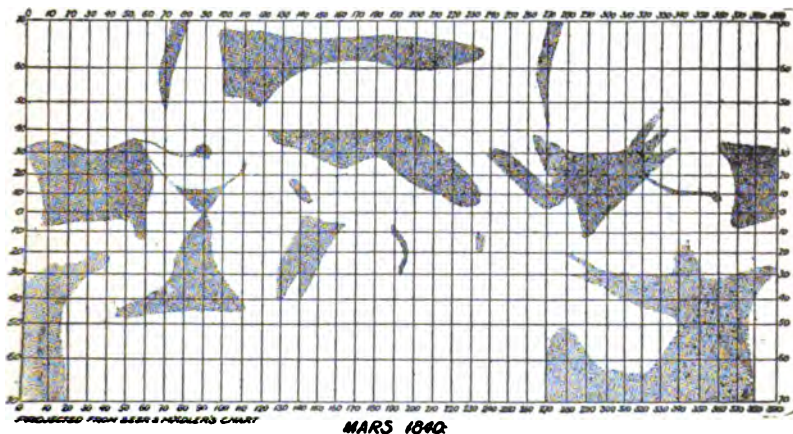
6. Near the end of the several periods are observations which mark the dawn of the next to come, making as they do adumbration of phenomena clearly to be revealed in the succeeding stage. Though not themselves the detection of details which characterize

the period, they make transition to them. Dawes thus made twilight to the third period in 1864; W. H. Pickering and the Lick observers to the fourth in 1892.

7. Distinct phenomena characterize the three periods. Patches of light and shade make the markings shown on the maps of the first stage of cartography. Of a piece though these patches are, their shapes appear well defined. At first one might suppose such to be due to the handicraft of the draughtsman and to possess no scientific value. But inspection of the several charts, one after the other, shows that the shapes are not artistic embodiments of ill-seen shadings, but are intrinsic traits of the shadings themselves, for chart after chart reproduces the same turns and twistings.

8. To see this we have but to take up in sequence the maps from 1840 to 1876. No. 1 of the series shows a cordon of patches

FIG. 1.

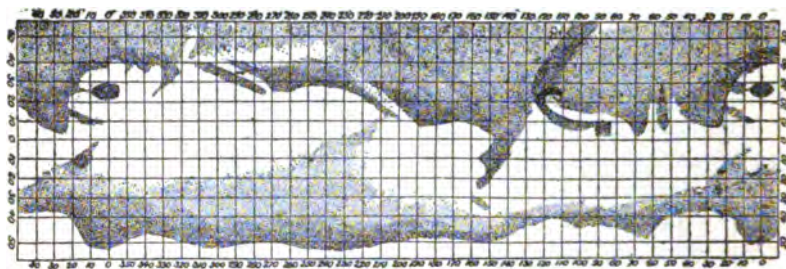


Map of Beer and Mädler, 1840.

stretching round the map at about  $30^\circ$  south latitude. Their height is greatest at  $90^\circ$  of longitude, and from this slopes down through  $360^\circ$  to  $20^\circ$  longitude, whence it gradually rises to the maximum. At the point of maximum is an oval marked out by broad shading on the south, by narrow penciling on the north, and holding a roundish dark spot in its centre. This is the Solis Lacus, the eye of Mars. To the right of it follows a leech-like patch, the Mare Sirenum and the Mare Cimmerium seen as one. After this comes

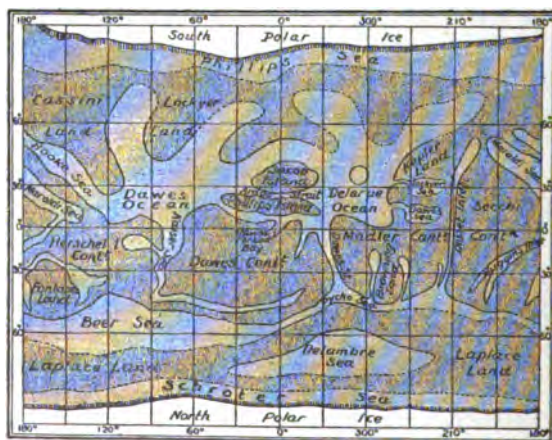
a large dark area in the shape of a funnel, the Syrtis Major. Then a ribbon ending in a scroll, the Sabaeus Sinus, the adopted zero point of Martian longitudes.

**FIG. 2.**



Map of Kaiser, 1864.

FIG. 3.



Map of Dawes, by Proctor, 1867.

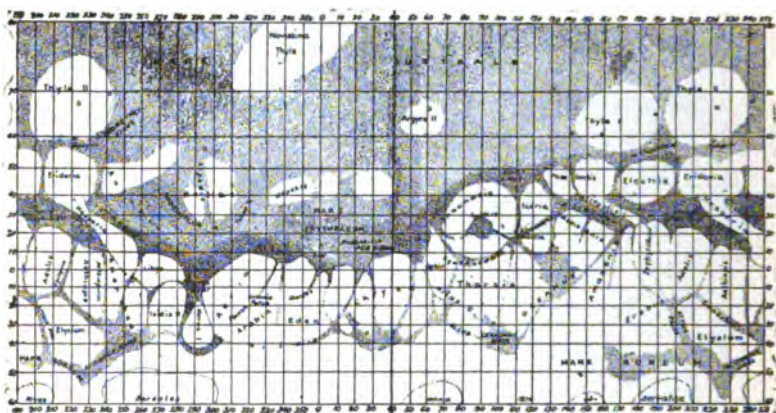
9. In map No. 2, Kaiser's, all these features can be followed, from the eye with its eyebrow and the curve of its lower lid down through the chain of seas back to the oculus again. The various other dark markings on the map can be similarly identified.





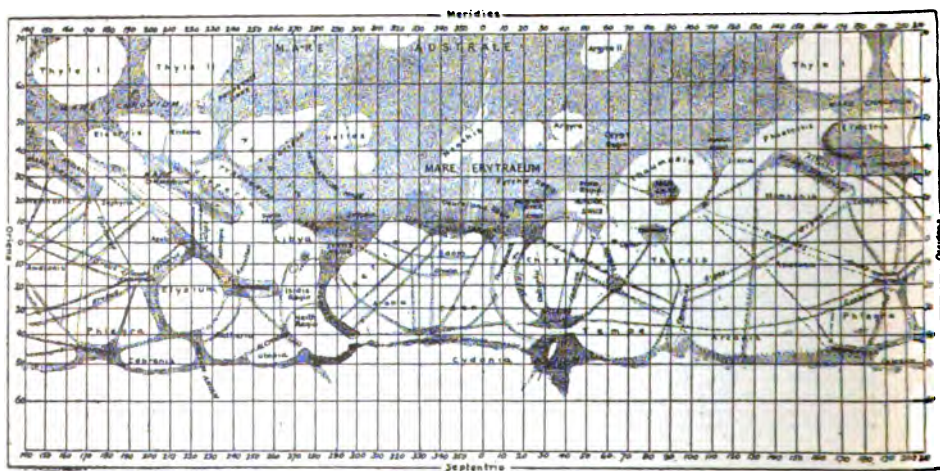
After the opposition of 1883-84 he drew only maps with the pole for centre, because of the tilt of the Martian axis which exposed the northern regions and hid the southern ones.

FIG. 6.



Map of Schiaparelli, 1879.

FIG. 7.

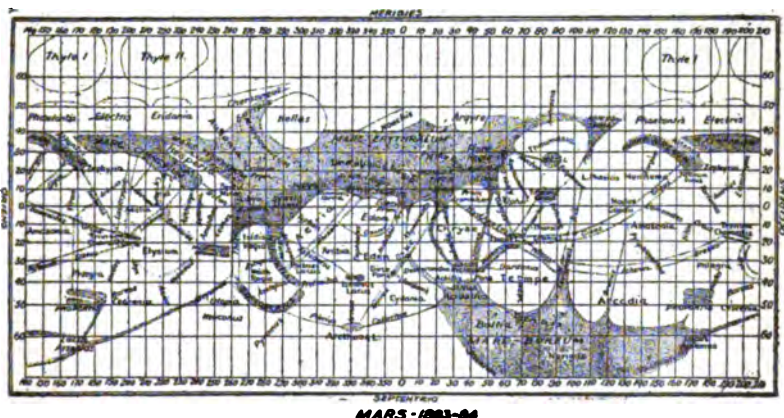


Map of Schiaparelli, 1881-1882.

The distinctive features of these maps are the "canals." The

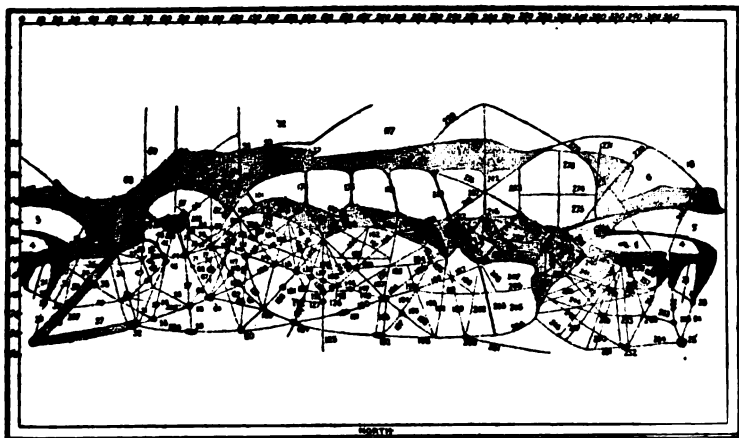
"canals" are objects as technical in character as they are in name, being quite unlike any other planetary detail. They are narrow lines of uniform width, of uniform direction and following usually

FIG. 8.



Map of Schiaparelli, 1883-1884.

FIG. 9.



Map of Lowell, 1894.

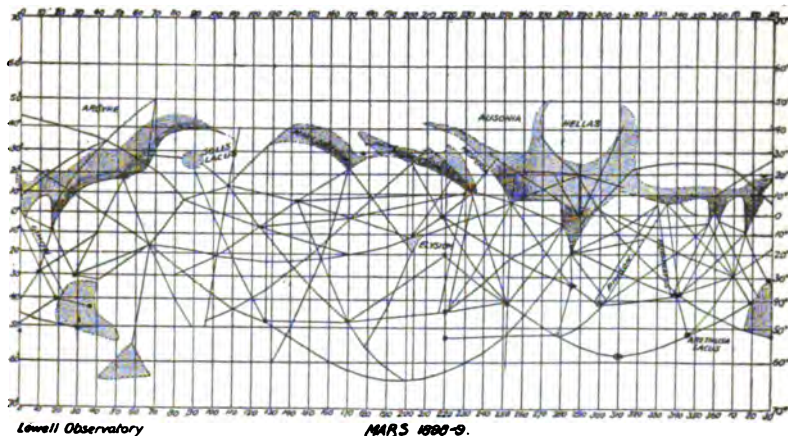
the arcs of great circles. Tenuity, regularity and intercommunication are the traits which make them *sui generis*. Such precision





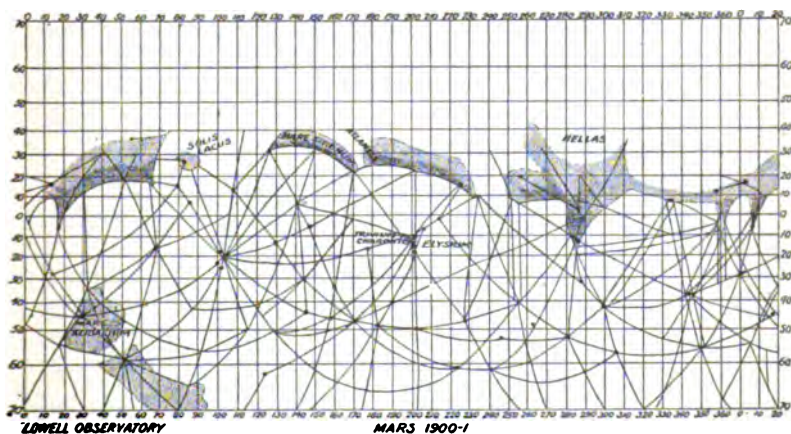
itself to be knotted with spots at its intersections. Many of the spots in the bright regions were detected by Pickering in 1892. Lastly, the two systems turned out to be connected together, the

FIG. 11.



Map of Lowell, 1898-99.

FIG. 12.



Map of Lowell, 1900-1901.

one system running into the other and marked by nick-like points in the coast line, thus making one united mesh of lines and knots superposed over the whole surface of the planet.

14. The history of areography may be thus summed up :  
1840-1876. Period of detection of large dark and light markings on the surface of the planet.  
1877-1892. Period of detection of "canals" in the bright regions.  
1892-1902. Period of detection of "canals" in the dark areas.

15. Three deductions follow an inspection of the whole series of maps :

I. The fundamental agreement of the series.

This is evident at once, but can perhaps be made more so by placing the later maps at a greater distance from the eye, upon which the fainter markings take on the look they would wear were the planet less well seen.

16. II. Evidence that the regularity of the "canals" was not due to predisposition on Schiaparelli's part, but was forced upon him by the objects themselves.

Comparing his own maps on the subject, it appears that an evolution took place in his perceptions. His first map, that of 1877, represents the "canals" as straits, more or less irregular, running up into the land. His next, made in 1879, depicts them narrower, straighter and decidedly more peculiar. That of 1881-82 shows them as fully developed geometrical designs, a character they never afterward lose.

Now, the fact that his representations of the canals grew in regularity as time went on, proves such character to have been no imputation on his part. Had he imagined it, he would have depicted the canals so to start with. As it was, increasing familiarity compelled him to recognize features which he had at first consciously or unconsciously ignored. We have here, indeed, a record left by himself of his own conversion to belief in the very qualities that make the canals so difficult of credence.

17. III. Evidence of an evolution in the detection of the markings from simple to complex. A steady progression in the matter of detail can be traced from its beginning to its end. And the progression is in increasing order of difficulty. The large dark patches are the easiest of detection, the Schiaparellian "canals" in the bright regions the next so, the "canals" in the dark regions the hardest. This is conclusively shown by the number of times each class was seen in the many drawings made at Flagstaff. It is here also evidenced by the way each map, while adding to, also corroborates its predecessor.

## SYSTEMATIC GEOGRAPHY.

BY W. M. DAVIS.

*(Read April 3, 1902.)*

1. Geography lacks System.
2. The Value of Systematic Geography.
3. The Content of Geography.
4. Physiography and Ontography.
5. Comparison of Geography with other Sciences.
6. Subdivisions of Physiography.
7. Classification of Land Forms.
8. Physiographic Classification involves Explanation.
9. Explanation involves Past History.
10. Value of Ideal Geographical Types.
11. Service of Deduction in Geography.
12. Contrasts of Biological and Physiographical Classifications.
13. Examples of Explanatory Description.
14. Distinction of Geography from Geology.
15. Dangers of Explanatory Description.
16. Framework of Physiographic Classification.
17. Complexity of Geography.
18. Relation of Physiography and Ontography.
19. Subdivisions of Ontography.
20. Regional Geography.
21. Conclusion.

1. *Geography lacks System.*—Geography has not as yet taken so much advantage from a systematic classification of the facts with which it is concerned as is the case with the biological sciences. The botanist or the zoölogist is greatly aided in observation and in description by the effort to refer every organic individual to its proper place in a comprehensive scheme of classification, whereby its relationships and its contrasts are most concisely set forth; and if he is for a time puzzled by a new species or by a form of uncertain position, he does not for a moment waver in his belief in the value of the principles of classification, but draws encouragement from the aid that it has already given him and perseveres until the systematic position of the new or uncertain species is made clear. The geographer on the other hand makes no such habitual use of

systematic methods. The classification that he uses is immature and imperfect; many classes of geographical problems are as yet hardly classified at all. It is with the intention of showing the need, the possibility and the value of systematic work in geography that this essay is presented.

If a geographer should come upon such an item as one of the narrow flood-plain scrolls sketched in Fig. 1, he might treat it in either one of two ways. He might describe it empirically as a local item of earth form, unrelated to all other items; or he might more or less consciously refer it to some appropriate place in a general scheme of geographical classification, whereby its origin and relationships would be made manifest. The geographer at

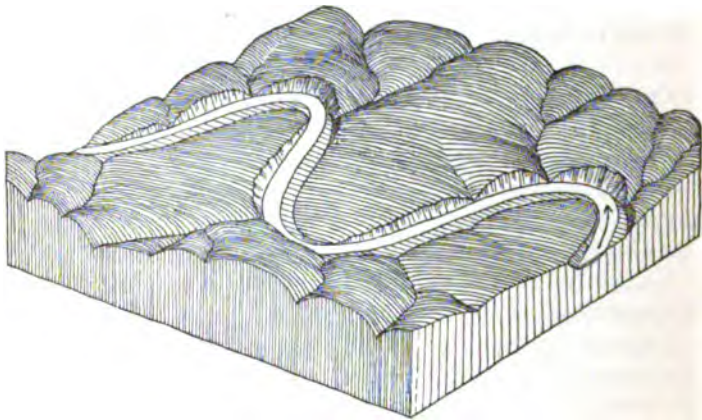


FIG. 1. A meandering valley with narrow flood-plain scrolls.

present generally attempts to pursue the second plan, as would be indicated by the use of such a descriptive phrase as "a narrow strip of flood-plain"; for the term "flood-plain" has a technical meaning and suggests that the observed example belongs with other more or less similar examples in a recognized class of geographical forms. If however we should question different geographers as to the relation of narrow flood-plain scrolls to flood plains of other forms, and as the rest of the scheme of classification in which flood plains form a single group, no approach to agreement would be found; for the venerable subject of geography has not yet established a well-coördinated system of classification for the

facts with which it is concerned. The classifications commonly employed are too often inconsistent, incomplete and immature—inconsistent in their different parts even as to the larger principles upon which their subdivisions are based; incomplete in not including nearly all the categories of facts which properly belong under geography; and immature in making too often only a small advance over the method and terminology of school days. The narrow flood-plain scrolls, such as are shown in the figure above, and such as exist in remarkably perfect development in the valley of the North Branch of the Susquehanna, would according to the methods of geographical description and classification usually current be given no sufficient statement as to their form, no adequate explanation as to their origin, no appropriate discussion as to their correlation with adjacent features, and no systematic treatment as to their share in constituting the physical environment of their organic inhabitants. Yet the flood-plain scrolls deserve due consideration in all these respects from any one who would clearly portray the geography of their district. Lack of consideration is not due to any serious difficulty that inheres in the systematic treatment here suggested, but simply to the habitually unsystematic character of geographical study.

It is the same with the organic items of the broad subject of geography. A farm or a village, a thicket or an ant-hill, a city on a bay, or a road over a mountain range is too often mentioned as if it were an isolated and ultimate fact, rather than as if it were a member of a class, exhibiting the peculiar response of certain kinds of organisms to their surroundings. Correlation between the envired organism and the physical environment is coming to be recognized as an essential part of geographical study, yet correlation is not habitual in the treatment of the organic division of the subject by those who would wish to be considered geographers; and as to classification of the correlations, there has as yet been made hardly a beginning. Still it can hardly be doubted that all organic responses are susceptible of a reasonably systematic grouping in relation to one another, and that every example would be better seen and appreciated if it were viewed in association with its fellows.

2. *The Value of Systematic Geography.*—It may be urged with much confidence that fuller attention to such items as narrow flood-plain scrolls, or to any one of the innumerable organic examples

that might be instanced, would be secured if geographers were habituated to treat all such items as forming parts of a whole, and to place every item in its proper place with respect to all others in a well-arranged system of classification. It is sometimes the case that the labors of the systematist are decried; but it is only when systematization is the master and not the servant of the investigator that it merits condemnation. The orderly arrangement of the events in the earth's long history is the goal of all geological study; for the facts of physical and structural geology must be dated in terms of geological chronology if their true relation is to be appreciated. So with geography: it stands to reason that any logical scheme for the classification of all the elements that constitute the content of geography would be of practical value in treating the innumerable items with which the geographer is concerned. The object of such an arrangement would not be to put facts away, out of sight, but to expose them in orderly fashion so that they can be most readily seen, to arrange them so that they shall illuminate and be illuminated by their neighbors. A result of double value would thus be gained. Every fact would be seen in logical relation to its fellows, and its fellows would be seen in logical relation to it. The attention of the geographer would thus be directed to a broadened consideration of correlations, instead of being allowed to limit itself to a narrow view of isolated and unrelated items. The work of the observer in the field would be greatly aided by the presence in his mind of an ideally full treatment for every kind of item that he encounters; unless indeed he has the good fortune to come upon an item previously unknown, and in that case the habit of systematic description already formed would come to his assistance in the effort to gain a full understanding of the novel element. There is no other means by which the general principles, the underlying philosophy of geography, can be so clearly set forth as by systematic classification.

3. *The Content of Geography.*—The first step in an attempt at classification requires an understanding as to the content of geography as a whole. Here at the very outset no general agreement can be expected to-day; but it is well to note that general agreement will probably be reached by following the trend of the progress by which geography has passed through two stages, now to enter upon a third stage of development. A hundred years ago, geography was the study of the earth and its inhabitants; explanation then

made a very small part of description, and even a teleological correlation of the organic and the inorganic divisions of the subject had not been introduced as a well-defined characteristic of its methods. With the progress of science during the nineteenth century, explanation came to constitute a larger and larger share of the descriptive chapters of geography; and from the time of Ritter, geography has been very commonly defined as the study of the earth in relation to its inhabitants, the relationship being exposed during the second stage of progress in the light of teleology, of which abundant traces may be seen to this day.

The third stage of geographical progress is marked by the introduction of two new principles during the last third of the nineteenth century. It thus came to be recognized that explanation must be systematically sought for in every department of the subject; for river courses as well as for winds and ocean currents; for moraines as well as for sand dunes; and it is further recognized that the relationship existing between the earth and its inhabitants must be explained under the broad principles of evolution. The earth with its lands and waters was not arranged for the convenience of its inhabitants; its inhabitants have had to learn, by more or less conscious experiment, to live upon the earth as they found it. As in so many other sciences, the evolutionary philosophy is of enormous practical import in geography. If the earth has not been expressly fitted to the convenience of its inhabitants, but if the inhabitants have had gradually to fit themselves to their slowly changing surroundings, how essential is it that we should study those surroundings minutely, with all the intelligence that has been awakened in the later days of man's history, in order to take the best advantage of them; how important is it that we should look carefully into the real nature of things, so as to avoid an environment that involves a hopeless struggle against the forces of nature, and to choose instead an environment in which the inexhaustible forces of nature will work to our advantage. With the adoption of the evolutionary philosophy, the content of geography can no longer be defined as the relation of earth and man, but as the relation of earth and life. The cleared roadway of a colony of pillaging ants becomes as properly a subject of geographical study as a railroad that connects centres of human population. Elementary geography may still deal with the simplest salient facts and place man conspicuously in the foreground; more advanced geography may include



examples of greater complexity, but always selecting important rather than trivial matters; but the investigator must study the trivial items along with the greater ones, and all must be duly scrutinized, described and classified.

4. *Physiography and Ontography*.—Let it then be here agreed that the whole content of geography is the study of the relation of the earth and its inhabitants. We thus see two prime divisions of the subject. One includes all the elements of the physical environment of life; the other all those responses which life has made to its environment; and in accordance with modern methods both of these divisions should be treated under the explanatory principles of evolution, inorganic and organic. It is the element of relationship between the physical environment and the environed organism, between physiography and ontography (to coin a word), that constitutes the essential principle of geography to-day. Mature, fully developed geography therefore involves the study of physiography and ontography in their mutual relations. Treated otherwise, the divisions of the subject lose coherence; they fall apart and are gathered up by various other sciences. It is only when they are bound together by the element of relationship that they constitute a reasonably connected body of study, as well unified a science as any other. In support of this principle, let us turn aside to note—as others have done—how largely the principle of relationship is serviceable in classifying the sciences.

5. *Comparison of Geography with other Sciences*.—All terrestrial substances, inorganic and organic, the study of whose relationships constitutes geography, are also the proper subject of study in relation to composition by the chemist: rock, water, air and organisms are all to be analyzed and classified as compounds. Again, all the activities in the world of geography are the appropriate subject of study in relation to energy by the physicist. Moreover, as fast as geography, chemistry, physics and the other sciences advance, their progress should be duly chronicled by the historian; for it is a sad mistake to imagine that the whole content of history is only the "politics of the past." From the discovery of America by Columbus to the discovery of a narrow flood-plain scroll on the upper Susquehanna by an early backwoodsman; from the migration of races across continents to the settlement of miller by a waterfall, there is no discontinuity. The historian must regard all such facts, great and small, as pertinent to his study of the sequence

of human events, even though he can make explicit mention of the greater ones only. The physicist must bring the behavior of a river in making its flood plains and of a stone in falling from a cliff under the domain of physical law, although he may not make mention of every flowing stream and of every falling stone in his systematic text-book. The chemist must discover all the kinds of changes in composition caused by the weathering of rocks; he must learn the composition of everything from the miller to his flour and his millstone. It is therefore not in terms of the things studied that a science can be defined, but only in terms of the relationships involved in the study. The things with which the geographer is concerned may also concern the physicist, the chemist and the historian; but as far as these things enter into the relation between the earth and its inhabitants, they constitute the content of geography.

It is particularly in relation to geology that geography has been needlessly confused. Geology is essentially a historical study; it is for the earth what history is for man. Geography, on the other hand, is distinctly not a historical study; what is often called historical geography might be much better called geographical history. Geography considers the relationship of existing conditions, inorganic and organic; and as far as the dimension of time enters into geographical methods, it is introduced not for the purpose of studying the sequence of events that lead up to existing phenomena—that belongs to geology or to history—but for the purpose of better seeing the existing phenomena themselves, as will be more fully shown below. Thus understood, geology and geography are closely related; it may be fairly said that geology culminates in geography, and that all geology consists of a sequence of paleogeographies. Surely, no geologist would dismiss the present condition of the earth and its inhabitants from consideration as constituting the last page in the recent chapter of historical geology. Ocean navigation and cable laying, city growth and railroad building deserve a place in the geology of the recent period on exactly the same ground that trilobite tracks and dinosaur prints belong in the record of the past. Conversely, every geographer should conceive all the geological history of the earth as involving a succession of geographies, horizontally stratified with respect to a vertical time line. All the processes of slow erosion, of volcanic eruption, of rising and falling lands, of organic adaptations, formed elements of

these successive paleogeographies, just as the slow depression of the Netherlands, the eruptions of Vesuvius and Pelee, the washing of neglected fields, and the migrations of Europeans into the open lands of America constitute elements of the geography of to-day.

The science of geography is therefore, like all other sciences, concerned with the relationships of things which, when they enter into relationships of other kinds, belong under other sciences, and which are known to be pertinent to geography not by their own qualities but by the relationship in which they are considered. It is the classification of the elements of a subject thus constituted that we have to consider.

It is not my purpose however to present here a detailed statement of a classification, but rather to set forth the nature of a classification which might, when expanded in a more technical geographical publication, afford suitable categories for all kinds of geographical facts. It will suffice therefore to indicate briefly the larger divisions of the subject, and to pursue only one of these divisions, namely the lands, into details.

6. *Subdivisions of Physiography.*—Geography as a whole has already been shown to consist of two chief divisions, physiography and ontography. Physiography has four chief subdivisions—the earth as a globe, the atmosphere, the oceans and the lands. Let us set aside for the present all but the last subdivision. The lands should first be treated as a whole, and their contrast with the other exterior parts of the earth considered. A notable contrast, of great significance in its ontographical relations, is found between the lands covered by the atmosphere, and the sea floors covered by the oceans. The latter are monotonously cold, dark and quiet, as well as remarkably uniform in shape and constitution; while the former exhibit a variety of forms, such as high and low, smooth and rugged, flat and steep, and experience a succession of changing conditions, such as wet and dry, calm and windy, hot and cold. The general weathering and washing of the lands, whereby their waste goes to make the gain of the sea floors, results in their being scored by many branching systems of valleys; this highly specialized kind of inequality being as significantly characteristic of the land surface as is smoothness of the blanketed sea floors. There is nothing new in all this, but geographers too generally fail to recognize these general features of the lands as the determining physical environ-

ments in response to which many an organic condition has been called forth.

The lands need subdivision into relatively small areas, for their forms vary greatly from place to place. It has long been habitual with geographers to describe and classify these forms empirically; but there is to-day a well-defined trend of opinion in favor of rational, evolutionary or explanatory description and classification, even though this more modern method has not yet found general acceptance in practical exploration. An eclectic system of subdivision, based on the suggestions of various writers, may be briefly stated as follows:

7. *Classification of Land Forms.*—Land forms are classed first as to kind, according to their rocky structure; thus one area may be of horizontal structure; a second may consist of broken and tilted blocks; a third may have a domed structure; a fourth may be folded; a fifth may be of volcanic origin, and so on.

Each kind of land form is then to be further classified according to its stage in the cycle of erosion, to which it is introduced by initial processes of deformation and (relative) upheaval, and through which it progresses by the action of weathering and washing towards an ultimate goal of obliteration in a featureless plain close to sea level, or in a smooth platform at an undetermined depth beneath sea level. There is to-day abundant warrant for asserting that the sequence of developmental stages through this destructive cycle of erosion is remarkably systematic, and that very effective description of land forms may be given by characterizing them simply as young, mature or old. This is therefore not a matter of abstract theory, but of practical convenience to the field geographer.

There is need of distinction between the inert land mass, offered to erosion by the telluric forces of upheaval, and the physiographic agencies by which the erosion is accomplished; the chief of the latter being river systems. There is again need of discriminating the forms assumed by the slow-moving waste of the land on the way to the sea, from the inert land mass on the one hand, and from the more active agencies of erosion on the other hand. With respect to the active water streams, the land waste is relatively inert and passive; but with respect to the inert underlying rock mass, the waste may be treated as part of the superficial river system. The latter treatment brings forth many interesting homo-

logies between water streams and waste streams, and from this arises a simple terminology for waste forms by which the power that words have of suggesting things is greatly increased.

It is still further necessary to distinguish between the several kinds of agencies that are chiefly responsible for erosion, as determined by climatic conditions. Thus far, a normal climate has been assumed, of sufficient rainfall to fill all depressions to overflowing and of insufficient snowfall to form glaciers. On one side of this norm there is the arid climate, where rainfall is small and vegetation scanty, and where the wind therefore takes a significant part in the work of shaping the land surface; here the whole surface swept by the wind corresponds to the bed of a water stream. On the other side is the glacial climate, where precipitation is chiefly in the form of snow and where drainage is chiefly in the form of glaciers; here the slender and nimble water streams of the normal climate are replaced by clumsy and sluggish ice streams, with the result of greatly increasing the proportion of drainage channel to drainage area.

Finally the border of the lands where they dip under the sea is attacked by waves and currents and appropriately carved; the cycle of shore erosion being just as systematic and helpful as the cycle of rain-and-river erosion. Each kind of land form, as determined by its rocky structure, exhibits forms peculiar to itself and appropriate to their stage of littoral erosion. Here, as in the normal and special cycles of subaerial erosion, such terms as young, mature and old are highly suggestive because of the systematic correlations of various elemental forms that they imply.

This system of classification is at present by no means fully developed, for it has been directly applied to but a relatively small part of the lands; yet it is so efficient where it has been applied that there is every reason to expect that it will be all the more efficient when it shall have been more widely applied and more fully developed. Some of its essential features may now be given fuller exposition.

8. *Physiographic Classification involves Explanation.*—Explanation of origin is regarded as essential to a complete description in this evolutionary method of physiographical classification. Not only must forms of simple and manifest origin, such as sand dunes and stream gorges, be explained; but all forms, difficult and obscure as their origin may be, must if possible be brought under

explanatory treatment. Geographers have been slow to accept this responsibility. True, they have long explained volcanoes by eruption, because eruptions have been witnessed; yet they have been habitually inattentive to the radial gorges by which extinct volcanoes are scored. While gorges and water-gaps are still sometimes ascribed to fractures and floods, most geographers of a fair degree of training explain them more wisely as the result of slow sawing by the streams that flow through them; yet most geographers are still accustomed to adducing a canyon and not a peneplain in evidence of the magnitude of the work that can be done by rain and rivers. There is therefore no more wholesome discipline for the field geographer than to insist on the necessity of explaining every part of the land form that comes under his observation. His courage in this respect should be whole-souled rather than half-hearted; and whatever difficulties he may encounter, the success already attained should strengthen his resolution to pursue his task until complete success is reached.

9. *Explanation involves Past History.*—It is evident however that an explanatory method of description involves the consideration of the past history through which land forms have come forward to their present estate; and thus the subject of physiography gains a strong savor of geological methods. Some geographers seem to be disconcerted by this consequence of the explanatory treatment. They appear to think that description through processes of origin involves too serious a trespass on the field of geology, and they therefore give explanation over to the geologist. But there is nothing novel in the trespass of one science upon the methods of another. The chemist is constantly employing physical methods; the astronomer is as constantly employing mathematical and physical methods. Hence no apology is needed if the geographer employs geological methods whenever they serve his purpose. The real point is that these geological methods serve a geographical purpose; the purpose, namely, of aiding the observation and description of land forms, for which the geographer is primarily responsible. Any methods that aid this end are appropriate. Much attention as the geographer may give to process and time as involved in the sculpture of land forms, his interest in these geological elements is not aroused simply from the hope of tracing out the sequence of events that the past contains, but from the expectation, well warranted by abun-

dant experience, of being better able to treat existing land forms by a rational instead of by an empirical method. It is the geologist who studies the past history of the earth as an end in itself; it is his duty to unravel all the tangled skeins of earth history, however far back they may lead him. The geographer is concerned with the past not as an end but as a means to an end; and he cares only for so much of it as shall serve his present needs.

10. *Value of Ideal Geographical Types.*—The addition of explanation to the responsibilities of the geographer brings with it the need of idealizing actual forms into type forms, for it is chiefly in terms of type forms that actual forms are in fine described. This is also a discouragement to geographers of the more conservative school, who have thought that geography was concerned only with matters of fact, immediately observable. They must however come to see that direct observation is entirely insufficient for the geographer's needs, for the simple reason that if he recorded only what he saw he would be overwhelmed with ungeneralized items. He must generalize in order to bring the observable items within the reach of descriptive terms, and as soon as he generalizes, the use of idealized types is practically unavoidable. Such types have long been in current use, but they have been too few and too empirically defined for the best results. They need to be greatly increased in number, and at the same time they must be correlated with structure, process and time; for only by following the path of nature's progress can we hope to store our minds with types that shall imitate nature's products. It may be fairly urged that the larger the store of types a geographer possesses, and the more careful and numerous the comparisons with nature by which the types have been rectified, the better progress can the geographer make in new fields of observation.

11. *Service of Deduction in Geography.*—But the geographer who adopts the explanatory methods in a whole-souled fashion will find himself called upon not only to imagine a large series of type forms; he must also call into exercise his deductive faculties and employ them to the fullest, if he would make the best progress in the newer phases of his subject, however purely inductive he has imagined it to be. In setting up a store of types, there is need of deducing one type from another at every step; and it may be confidently urged that whoever hesitates to recognize this principle will fail of his effort to describe through explanation. But as a

matter of fact, geography has some time been more deductive than geographers have supposed it to be ; and the newer phase of the science is not characterized so much by introducing deduction for the first time, as by insisting on its whole-souled acceptance as an essential process in geographical research.

It is only by giving the fullest exercise to the faculties of imagination and deduction that the cycle of erosion becomes serviceable. Here the geographer who hesitates is lost. Not only should the ideal cycle be followed in imagination through all its gradual changes on a large variety of structures, but the special cycles of arid and of frigid climate must be similarly treated ; and then each of these cycles must be broken up by earth-movements into partial cycles and episodes. It is only in this way that the scheme of the cycle gains a serviceable elasticity ; and it is highly significant that among those geographers who find the conception of the cycle unfruitful is one who has, with more candid indication of his unexercised imagination than he may have supposed, likened it to a "strait jacket."

Those who have not attained some fluency in the verbal translation of the various stages of normal and special, simple and interrupted cycles can have little understanding of the practical aid that is derived from this method of description. The empirical geographer, unsupplied with a store of carefully imagined and well-defined type forms, sees only what is before him in the field—if indeed he sees so much as that. The geographer who calls the faculties of imagination and deduction to his aid, draws from his mental store one type after another in the effort of matching the explained ideal forms with the actually observed forms. Thus comparing the partial view of the landscape, as seen by his outer sight, with the complete view of the type as seen by his inner sight, he determines, with great saving of time and effort, just where his next observations should be made in order to decide whether the ideal type he has provisionally selected fully agrees with the actual landscape before him. When the proper type is thus selected, the observed landscape is concisely and effectively named in accordance with it ; and description is thus greatly abbreviated. It goes without saying that this relatively advanced stage of investigation is not to be reached hastily ; that abundant and elaborate description of actual and of type forms in empirical terms, without a trace of explanation, should be demanded of the tyro who aspires to become an



expert ; for in no other way can proper training in the use of types be secured.

12. *Contrasts of Biological and Physiographical Classifications.*—

It may be worth while to note explicitly that there is little resemblance between the basis of the physiographic classification of land forms, here outlined, and the phylogenetic classification of organic forms now in vogue. In the latter case resemblance is inherited by actual derivation from common ancestors ; and if similar forms arise as a result of similar environment, independent of relationship by descent, this only serves to emphasize the rule by pointing to the exception from it. In the former case, resemblance is due to repetition of physical conditions, and inheritance naturally has no part to play. Similar structures, acted on by similar processes, at similar rates for similar times will have similar forms ; but as structures, processes, rates and times are all variable, it is not to be expected that identical forms should be developed. All the more need, therefore, of developing a method of rational generalization, whereby the essential features of a landscape may be seized upon as the basis for its description, while the insignificant elements of a landscape may be set aside. It should further be noted that while hybridization is of very limited range among organic forms, there is no limit to it in land forms. All sorts of structures are combined in all sorts of ways and acted on by all sorts of processes at various rates for different periods. This is indeed one of the chief causes of difficulty in physiographical description. Without free crossing of species, the variety of landscape would be much lessened. Physiography would then be easier and less interesting than it is now.

13. *Examples of Explanatory Description.*—The flood-plain scrolls illustrated in Fig. 1 may be instanced as examples that come very easily under the explanatory description of land forms. It has been ascertained with a high degree of certainty that a winding river, revived to renewed downward corrosion by the uplift of its basin, will increase the radius of curvature of its bends and push every bend down-valley while it is cutting down to grade with respect to its new baselevel. If the river had a meandering course when the uplift occurred, the increased width of the meander belt will be shown by the gentle slope of the spurs that enter each meander, as well as by the abrupt bluffs by which each meander is enclosed ; while the down-valley advance of the meander system will be shown by the extension of the enclosing bluff with decreas-

ing height along the up-valley side of each spur, so that the spurs have an unsymmetrical cross section as shown in the figure. No flood-plain is developed before grade is reached; but as soon as this delicately organized condition is attained, further valley deepening is practically stopped, although the meander belt continues to widen, and the curves continue to advance slowly down-valley. As a result, narrow strips of flood plain in scroll-like patterns must be developed; a scroll will begin by lapping around the end of a spur; it will then follow along the gentle slope on the down-valley side of the spur and end with reversed curvature shortly after reaching the next enclosing bluff. As time goes on, the spurs are more consumed and the scrolls are widened. The spurs may be trimmed into sharp cusps, and later reduced to blunt cusps, and then the scrolls must have widened into shield-like patterns. As the river swings more and more freely and opens a valley floor of greater breadth than the meander belt, the separate flood-plain shields are joined; further than this we need not trace them here.

Now it is not conceivable that geographical items as systematic as these flood-plain scrolls should be treated empirically, after their origin and their development has once been made out. It suffices in describing the meandering part of the valley of the North Branch of the Susquehanna to say that it has reached the stage of narrow flood-plain scrolls; for on saying this, the sloping spurs and the enclosing bluffs at once come to mind as elements of form that are necessarily correlated with the flood-plain scrolls. The meandering valley of the Rance in Brittany shows a succession of narrow scrolls in the most orderly arrangement. The valley of the lower Seine by Rouen possesses broader scrolls; nearer the river mouth, where the tides run strong, the spurs are greatly reduced. The curving valley of the Evenlode, a diminished headwater of the Thames system in the Cotteswold hills of England, has sharply trimmed spurs which prove that the Evenlode was not beheaded until a somewhat advanced stage of valley development was reached. The diminished stream now straggles irregularly about the open valley floor. The valley of the Lot in southwestern France may be described as having nearly reached the stage of consumed spurs in one cycle, when a moderate elevation introduced a new cycle in which the stage of wide scrolls is now reached. The essential features of the valley are thus concisely indicated, although many individual variations from the suggested type are to be found.

14. *Distinction of Geography from Geology.*—If the explanatory method is adopted as appropriate for the physiographic description of meandering valleys in the narrow scroll stage, the same method should be adopted for all other stages of valley carving and for all other land forms as well. The orderly action of natural processes through a portion of past time is implied in such a phrase as "the narrow scroll stage," and it is similarly implied in saying that the Alleghenies of Pennsylvania are of corrugated mountainous structure, essentially baseleveled in a former cycle; then broadly elevated and thus standing long enough for the weaker strata to be etched out as lowlands, leaving the harder strata to stand up as even-crested ridges; and then again moderately elevated long enough ago for the valley lowlands to have now reached a submature stage of dissection. The descriptions of the Susquehanna valley and of the Pennsylvania Alleghenies differ in the quantity of past process and of past time involved; but such a difference is only of degree, not of kind. If all the stages of development through which the Pennsylvania Alleghenies have passed are traced out for their own sake, as much attention being given to one stage as to another, then the study is truly geological. If the changes of the past are introduced only in so far as they illuminate the present, and with no other object than to secure such illumination, then the study is geographical. It would be as much a mistake to regard such study as geological as it would be to say that a chemist is studying physics when he uses a balance to weigh a precipitate, or that he is studying mathematics when he calculates atomic weights. He is truly enough for the time employing physical and mathematical methods, but he is studying chemistry. It would be no more just to regard the explanatory description of flood plains as belonging under geology because it has to deal with past time, than to treat it as belonging to the study of physics because it involves the application of physical principles in the flow of a stream, in the corrosion of its bed and banks and in the transportation and deposition of detritus; and surely it would be no more appropriate to regard such a study of flood plains as a part of physics than it would be to take away the spectroscopic study of the stars from astronomy.

15. *Dangers of Explanatory Description.*—It is sometimes objected that the explanatory method of description is dangerous, because the observer who seeks to add explanation to observation

may be led to think that he sees things that do not exist. There is certainly some danger of this kind, but it can be greatly lessened by good training—without which the explanatory method is indeed valueless—and in compensation for the little danger that remains, there is the great increase in the thoroughness and accuracy of observation that results from bringing forward the various idealized types to be confronted with the facts in the field. If doubt finally remains, it may be expressed by the phrase, “as if”:—The Susquehanna valley looks as if it were in the stage of narrow flood-plain scrolls. The initiated reader is thus concisely put in possession of the most probable conclusion as well as of the doubt that accompanies it. As a matter of practical experience, it may be urged that the gain from attempted explanation far outweighs its danger; and in illustration of this conclusion reference may be made to the curious case of the Connedogwinet, a branch of the main Susquehanna opposite Harrisburg. The branch has an unusually serpentine course, and the tangents between its curves are of extraordinary length. On visiting it in the spring of 1901, I expected that it would show normal narrow flood-plain scrolls; but as a matter of fact, its scrolls were found to be distinctly abnormal, inasmuch as they are nearly all on the down-valley side of the tangents. Truly, this is not a matter of great geographical consequence; the farmers would cultivate the scrolls, on whichever side of the tangents they might lie; but it is certainly of some physiographical interest to note their abnormal position, because it contradicts a generalization that is well supported by the repeated occurrence of examples in various parts of the world; a generalization that is fully explained by simple processes, perfectly accordant with the laws of stream flow. No explanation of the abnormal situation of the Connedogwinet scrolls has yet been suggested; indeed, as far as I have read, no mention of them as abnormal features has ever been made. Their peculiar arrangement seems never to have been noticed until it was brought out as an exception to the rule of flood-plain development. This example may therefore be taken to show that, far from there being serious danger of seeing imaginary facts by the light of theoretical explanation, a well defined conception of ideal types is a positive aid in correct observation.

16. *Framework of Physiographic Classification.*—If the explanatory method of physiographical description were adopted, it would result in the construction of a mental framework on which all

imaginable types would find their appropriate place in a systematic arrangement. Each of these types might be considered to be the label on a pigeon-hole ; and actual examples would be placed in their appropriate pigeon-hole as fast as they were collected. The compartments designed for common examples would soon be filled ; while others might long remain empty. Such a plan as this greatly promotes systematic observation, for the very fact that a certain pigeon-hole contains no actual form corresponding to its idealized type urges the observer to search for the missing example in districts where its occurrence is most probable. Revision of an idealized type would naturally be made whenever an example resembling it was found ; for however deductive the method of developing types may seem when here stated in the abstract, the actual progress of this sort of study involves repeated oscillations between induction and deduction, in which each process aids the other. The types are therefore not to be thought of as fancy pictures, unreasonably constructed by an ungoverned imagination and arbitrarily fixed by obstinate deduction. They should be the very best imitations of nature that the well-trained mind can construct, and they should be held subject to constant revision and correction as fast as observation is extended.

The conservative geographer will hesitate to construct a framework in which his types shall be more numerous than his examples. Indeed it sounds at first rather presumptuous to say that the variety of idealized types can exceed the variety of nature ; but there is no doubt that it can. The earth is after all not so very large ; and when all the examples of physiographic items that it contains shall have been studied out and systematically arranged, it will be easy enough to construct imaginary types that belong between two actual examples. Even if all the items that have existed in all the paleogeographies of the earth's history were brought into systematic arrangement, it may be doubted whether they would fill all the pigeon-holes of a well-imagined framework, so easily can the imagination conceive of a type intermediate with respect to any two neighboring examples.

It is therefore plainly a profitable exercise for the systematic geographer to elaborate his systematic framework as far as possible ; to increase the number of its little compartments, each bearing an appropriate label ; to arrange all the compartments in as systematic an order as he can develop ; and to devise every means—verbal,

graphic or mechanical—by which the framework shall always be at his service for practical use. Its value will increase with every step that is taken towards a vivid realization of its imaginary contents. It may seem cumbersome as long as it is unfamiliar; but when it is familiarly known it becomes an indispensable aid in practical work.

17. *Complexity of Geography.*—The whole current of thought changes when the ontographic half of geography is taken up. The training that is here necessary must be gained largely through biological study, while the training for the study of the earth as a globe is associated with astronomy, for the atmosphere with physics, for the oceans with hydrostatics and hydrodynamics, for the lands with geology. Whether this diversity of discipline is an advantage or not need not be answered; it is certainly a necessity. It is perhaps true that geography has, by reason of its many-sidedness, a more complex content than any other science; but if so it merely occupies a rank that would be otherwise held by some other subject; and certainly there is no impropriety in standing at either end of the list in this respect. Astronomy ranks well among the sciences, yet it now calls for mathematical, physical and chemical discipline; and if the change of color on the face of Mars follows his seasons it may be necessary to add a biological discipline as well.

Some have feared that the various parts of geography might fall asunder from their diversity of content and of discipline. So they undoubtedly would, but for the bond of relationship that holds them so strongly together. It may perhaps come to be wise for the geographer to follow the example of those engaged in other sciences and limit his attention to one part of his subject. Just as there are mathematical and physical astronomers, inorganic, organic and physical chemists, students of ancient, modern and many other groups of languages, so there may advisedly be physiographers and ontographers, instead of geographers; but all this is of secondary importance. Geography certainly has its inorganic and its organic side, and both must be understood by any one who would claim to be a thoroughly trained geographer, versed in the relationships by which the physiographic and ontographic sides of the subject are held together. The reason that so few persons can to-day rightly claim such standing is not so much because there is any inherent difficulty in the subject on account of its breadth and its complexity,

as because the subject is not maturely developed; but this is an aspect of the question that I shall elsewhere consider.<sup>1</sup>

18. *Relation of Physiography and Ontography.*—Unlike physiography, which has been recognized as an essential constituent of geography for many years past, ontography has to-day hardly gained an established position. It is best represented in Ratzel's *Anthropogeographie*, but this subdivision of the science is concerned only with the human element, and that is manifestly but a part of the total content of ontography. It is approached in ecology, but none of the many definitions of that term cover all that is here intended, for ontography is meant to include all the responses of organic forms to their physical environment, whether in physiological structure, in individual behavior, or in racial habits. Whether there is need of this new term, whether it will survive or not, it serves a present purpose in bringing clearly forward the organic half of the geographical whole.

The subdivision and classification of ontography has not yet been well accomplished. Before it can be well done, there must be much searching; but we may look forward to a time when all ontographic items shall be arranged on an ontographic framework, in which every compartment shall have for a label what biologists might call a type response. I am persuaded from much profitable experience with the physiographical framework that a corresponding advantage will come from the construction and familiar use of a similar framework for ontography. Still more: the two frameworks might be brought face to face, and lines might then be drawn between them, connecting cause with effect, effect with cause. If then a plane were passed secant to all these lines of relationship, all the content of geography might be projected along the lines upon it. If the plane were placed near the physiographic framework, there would be groups of points, where numerous radiating lines departing from some dominant physiographic control pass through the plane on their way to various ontographic effects. If the plane were passed near the ontographic framework, the grouping of numerous points of intersection would serve to indicate those organic forms which respond to many physiographic controls, while isolated points would indicate forms that respond to few. Accord-

<sup>1</sup> National Association for the Scientific Study of Education, Proceedings of the Minneapolis Meeting, July, 1902.

ing therefore as the geographical plane is placed nearer to one framework or to the other, the presentation of the total subject might be made primarily physiographic and secondarily ontographic, or the reverse.

19. *Subdivisions of Ontography.*—It is not an ontographic classification, but the nature of such a classification that can here be set forth to best advantage. There should be two chief subdivisions; the first includes those responses that were initiated ages ago and maintained by inheritance till to-day because their controls are persistent; the second, those of relatively recent origin. Further subdivision might be made in accordance with the standard classifications of botany and zoölogy, in which the responses of all kinds of plants and animals to physiographic controls would be taken up in their natural order. But in view of the repetition of similar responses in many different classes of organisms, it will be here more convenient to follow a physiographic order in the ontographical classification. Examples of long-inherited responses will be mentioned first.

As inhabitants of an earth whose mass is very much greater than that of all its organic population, plants and animals very generally show a response to the action of gravity in their attitudes as well as in their structure. As inhabitants of an earth whose opaque surface is illuminated from without, the distribution of color in plants and animals is often closely associated with the response to the downward action of gravity. As occupants of an earth whose surface is nearly globular, plants and animals have been allowed a much wider migration than would be possible for the occupants of a very irregular body, on whose surface gravity would vary greatly. None of these responses are doubtful as to origin or difficult as to comprehension; they ought to be introduced in the elementary study of the earth as the globe; and their almost universal omission from that chapter of geography affords immediate illustration of the little thoroughness with which the subject is treated. Perhaps these matters have been omitted because they are regarded as of less importance than the names of the branches of Siberian rivers; but if so, a very singular standard for the measure of importance has been accepted. Many other long-inherited responses to the physical features of the earth as a globe might be instanced, but space is lacking for their presentation.

One of the most universal of all organic habits, that of breathing



free oxygen, must be regarded as the long-inherited response to the presence of oxygen in the free state, whether mixed with other gases in the atmosphere or dissolved in the waters of the ocean. Organs of flight, to-day characteristic of many insects and birds, are extraordinary devices for movement through the air; this may seem a valueless truism to some, but it must be explicitly stated if the ontographic framework is to be thoroughly constructed, and if conscious attention is to be aroused to it. Vocal organs are responses to the extreme elasticity of the air; human speech may be reckoned among the responses of modern acquisition under this class. The adoption of blue as one of the primary colors of the spectrum is a modern response to the color of the sky; a physiographic fact that has waited long for its ontographic mate. Pollen grains, spores and innumerable microscopic organisms of great importance in the economy of the nature, exhibit in their minuteness a response to the small sustaining power of the winds that bear them about. If climate were here considered as well as these simpler physiographic features of the atmosphere, the number of ontographic responses in this class would be greatly increased.

The greater buoyancy of water than of air has a notable response in the absence of feet among most of the swimming animals of the ocean. The flying animals of the atmosphere, on the other hand, always have legs to sustain them when they alight on the ground from the little sustaining air. The same contrast between water and air must account for the much greater size of the floating inhabitants of the ocean than of the blown-about organisms of the atmosphere. While the more opaque animals of the sea usually have a darker dorsal and a lighter ventral surface, many of the floating animals find relative safety in imitating the transparency of the waters in which they float. It is the monotony of the cold, smooth, dark and quiet ocean bottom that has doomed it to be the home of the less intelligent organisms; while the variety of the lands has promoted the development of the most remarkable instincts and the highest intelligence among their inhabitants.

The separation of the lands into several large continental masses has led to the division of mankind into races; and closely associated with this division into races go many peculiarities of government, religion and degree of civilization. All this is most intimately connected with that phase of ontography commonly called political geography; and yet so arbitrary and irrational is

the traditional classification of geographical topics that the division of mankind into races is commonly taught under physical geography. The races may be fairly enough introduced there as illustrations of ontographical consequences following from physiographical controls; but to regard them as essentially physiographic topics shows a regrettable failure to recognize the essential quality of geographical discipline.

The simple physiographic factor of distance is of great importance. It involves the separation of the people of a race into many families, and thus is a determining cause of difference of language and of many other habits. The unevenness of surface exhibited in mountain ranges is of small measure in comparison to the dimensions of the earth, and yet it suffices to make movement so difficult that the occupants of one valley may have a distinctly different dialect from those in a neighboring valley. How circumscribed would have been the migrations of the earth's inhabitants if the height of mountain ranges were a large part of the earth's radius! The sheet of loose rock waste by which the lands are so largely covered not only supports the growth of plants, but has been adopted as a home by many kinds of animals; and according as the waste is a coarse talus lying on the steep slopes of a young mountain side, or a fine, deep soil blanketing a peneplain, its occupants are of different kinds. Instances of this kind might be extended without number.

Examples of modern responses to physiographic controls are best found in those new-fashioned characteristics of mankind that are seen in sites of settlement, routes of travel, and in the development of trades and of commerce.

Settlements in deserts offer particularly striking illustrations of the dependence of population on water supply. Settlements on rivers are largely determined by head of tide, by falls, and by fords. Settlements on coasts are influenced by protection from the open sea, and by ease of access from sea and land. The routes of trade and commerce are guided by physiographic factors literally at every turn. Straight roads are laid out on plains, but winding valleys are commonly followed in regions of strong relief; tunnels are driven through mountains; short-cuts are made through isthmuses. Here as before, illustrations are endless; yet abundant as they may be, they have not yet been well classified. At the present day, ontography is less developed than physiography.

Many examples are individual rather than generic. It was the shoals remaining where morainic islands once arose that turned the Mayflower northward from a course that might have led her south of Cape Cod to New Amsterdam ; it was the greater height of the mainland where the moraines of Manomet were piled upon it that led the Pilgrims from their first landing at Provincetown to the quiet harbor of Plymouth. The varied course of human history affords innumerable examples of this kind. It would be profitable to make a long list of them, to classify the items thus gathered, and to select the best examples of various classes for presentation as types. A geographer who was well informed regarding such types would undoubtedly be more observant in his travels than many travelers are to-day. He would be continually asking questions and finding answers where he is now silent.

20. *Regional Geography*.—It is in the prevalently unsuccessful treatment of regional geography that the undeveloped condition of systematic geography is made most apparent. It is well recognized in the organic sciences that only after a general understanding of systematic botany or systematic zoölogy is gained can a profitable attempt be made to describe the flora or the fauna of a limited district. The same principle undoubtedly obtains in geography ; yet nothing is more common in geographical literature than an attempt to treat the geography of a certain region before any thorough system of geography has been agreed upon. This error is in the way of being corrected, but it is still a prevalent error. In texts on physical geography, for example, it is still common to find an attempt made to describe the physiographic features of the several continents before any sufficient understanding has been gained as to the nature of physiographic features. The year of study commonly allotted to this subject in the schools is none too long for a sound systematic course, and by no means long enough for the addition of a regional course as well. Systematic physiography may be vivified by the introduction of many well-selected examples from various parts of the world, but there is not time in a single year to present a substantial account of the continents or even of a single continent in addition to the systematic account of the whole subject.

21. *Conclusion*.—The practical conclusion of all this is that it is the nature of geography as a whole, rather than the accumulation of unassorted and uncorrelated items, that demands the attention of

geographers. Careful analysis and arrangement of the content of the subject is as greatly needed as the exploration of unknown lands. It must be remembered, however, that the object of analysis and classification is to render practical aid in the understanding of geographical items, old and new. There should be no hindrance placed in the way of the active pathfinders who seek to enter unknown lands; but there should be every encouragement given to those who believe that some of the unknown elements of geography may be discovered without going far from home.

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*Stated Meeting, April 18, 1902.*

President WISTAR in the Chair.

Present, 16 members.

Letters accepting membership were read from

Dr. John A. Brashear, Allegheny, Pa.

Dr. Andrew Carnegie, New York.

Prof. William B. Clark, Baltimore.

Dr. Hermann Collitz, Bryn Mawr, Pa.

President Arthur T. Hadley, New Haven.

Prof. George E. Hale, Williams Bay, Wis.

Dr. C. Hart Merriam, Washington.

Prof. Theodore W. Richards, Cambridge.

Prof. Felix E. Schelling, Philadelphia.

Prof. Robert Henry Thurston, Ithaca, N. Y.

Prof. Robert S. Woodward, New York.

Mr. Thomas Willing Balch presented, on behalf of his brother and himself, the MS. account book of the first "Philadelphia Assembly," 1748, and read a note thereon.

Mr. Alden Sampson read a paper on "The Ruins of Palmyra, with a Brief Consideration of the Ancient Estate of that City."

THE FIRST "ASSEMBLY ACCOUNT"  
—PHILADELPHIA, 1748.

BY THOMAS WILLING BALCH.

(*Read April 18, 1902.*)

John Swift, a Manager and the Treasurer of the First Assemblies, was the eldest child of John Swift and Mary White, his wife, of London. He was born in 1720. He went to England together with his younger brother, Joseph Swift, where they visited their uncle, John White, of Croydon, now a part of London. Returning to America in 1747 he was, as a merchant of Philadelphia, very successful. He was a member of the Common Council from 1757 to 1776, and Collector of the Port of Philadelphia from 1762 to 1772. During the latter part of his life he lived at "Croydon Lodge," in Bucks County, where he died in 1802 and was buried in Christ Church burying ground, Philadelphia, January 14, 1803.

The Philadelphia Assemblies began in 1748, only five years after the organization of this Society. They are, I believe, the oldest dancing organization in the country, their only serious rival, the Saint-Cecelia Society, of Charleston, dating from several years later. During the winter of 1748, six Assemblies were given under the management of four Directors: Lynford Lardner, John Inglis, John Wallace and John Swift. There is a tradition in the Swift family that the *first* meeting at which the Assemblies originated was held at John Swift's house. There were fifty-nine subscribers in all, and as an invitation was extended to the families of every head of a family who subscribed, probably some two hundred persons were eligible to attend the dances. The subscription was two pounds sterling. In 1879, Mr. Charles Swift Riché Hildeburn, a descendant of John Swift, the Manager and the Treasurer, and Mr. Richard Penn Lardner, a descendant of the first Lynford Lardner, the Manager, presented to the Historical Society of Pennsylvania two documents intimately connected with the First Assemblies. Mr. Hildeburn gave the rules to govern the dances, and Mr. Lardner gave the list of the original subscribers.

A third manuscript relic of those gay festivities is the account book kept by John Swift. It descended through the lineal descendants of John Swift to that learned and accomplished antiquarian and bibliophile, the late Mr. Hildeburn, a member of this Society.

It is a small, thin book, and Mr. Swift used it originally for some of his own accounts, and for some land transactions for his younger brother Joseph. On one cover he wrote: "Account book 1746." When the Assemblies were instituted and his fellow-managers chose him the Treasurer, he turned to the other end of this little book and there kept the "Assembly Account." Owing to age and neglect—indeed, had it not been for the keen antiquarian eye of Charles Hildeburn, it would probably long ago have gone to the paper mill—the Account Book is much worn and somewhat injured. But now it has been treated by an expert, and every sheet covered with silk so as to guard it against any future weathering of time.

An examination of the account shows that the six Assemblies of 1748 were far less costly than the two large balls that are now given annually at the Academy of Music; or, for that matter, even the three balls that were held each season about fifty years ago at Musical Fund Hall. In one respect, however, those old worthies were not behind the present generation, for taking all things in proportion they provided rum liberally. The record kept by Mr. Swift is somewhat injured, so that it is impossible to state exactly how much he disbursed, but the whole cost of the six dances seems to have amounted to a little more than £130. As there were only fifty-nine subscribers at forty shillings each, which gave a total of £118, the Managers doubtless, as so often happens nowadays in all sorts of social and philanthropic undertakings, had to put their hands in their own pockets. A few extracts from the expenses show the modest and simple character of the entertainments:

	£.	s.	d.
" pd Mary Dicas for China & Candles as per Acct ending 7 <sup>th</sup> March . . . . .	8	15	6
pd Mr. Inglis for Sundries . . . . .	—	19	—
16 <sup>th</sup> [March] pd for Bisket . . . . .	—	9	6
pd Musick . . . . .	1	10	—
pd Diana . . . . .	—	2	6"
And again :			
" pd for 2 Gallons Spirit . . . . .	—	15	—
pd Sharper 5 nights attendance . . . . .	—	18	9
pd. Greek for attendance . . . . .	—	7	6
pd. Mr Inglis for rent . . . . .	20	—	—"

The Managers of the first Assemblies had to pay a tax, both to the city and to the county, as may be seen by turning to Mr. Swift's Account Book; but as the book is there somewhat torn, it is impossible to know how much.

From the time the Assemblies were first organized to the present, they have continued with pretty general regularity except when interrupted by war or other serious drawbacks. They have been held in various places, and the names on the list of subscribers have changed very much. Many of the Quaker families—such as the Rawles, the Norrises, the Logans, the Whartons, etc.—that owing to their faith kept aloof at first from such gay and frivolous pastimes, later joined in with the Shippens, the Willings, the Swifts, the McCalls, the Hopkinsons, the Lardners, the Francisces, the Bonds, the Lawrences, and others who were among the first list of subscribers. And some of the old names *alas* have died out.

It is not inappropriate on this occasion to recall to mind a few of the ladies who took part in those entertainments in the latter half of the eighteenth century. Lieutenant-Colonel Joseph Shippen, a graduate of Princeton, who was elected a member of this Society, January 19, 1768, and who served under Forbes in the capture of Fort Duquesne, and was a generous patron and benefactor of Benjamin West, has portrayed for us a charming picture of some of the belles that reigned supreme at the Assemblies in his day. In the "Lines written in an Assembly Room," which he wrote at least as early as 1774, and very probably in the sixties, he says:

" With just such elegance and ease,  
Fair charming Swift appears;  
Thus Willing, whilst she awes, can please;  
Thus Polly Franks endears.

\* \* \* \* \*

" With either Chew such beauties dwell,  
Such charms by each are shared,  
No critic's judging eye can tell  
Which merits most regard.

" 'Tis far beyond the painter's skill  
To set their charms to view;  
As far beyond the poet's quill  
To give the praise that's due."

The invitation card to the Assemblies for 1790 for Colonel Ship-

pen's daughter Mary—better known as "Polly" Shippen—has been preserved, and reads as follows :

"PHILADELPHIA ASSEMBLY, 1790.

The Favour of Miss P. Shippen's  
Company is requested for the Season.

J. M. NESBITT,	W. STEWART,
GEO. MEADE,	JOS. REDMAN,
JOHN SWANWICK,	GEORGE HARRISON,

*Managers."*

Another card for the season of 1850, when three Assemblies were given at Musical Fund Hall, is thus inscribed :

"ASSEMBLIES.

"The Honor of  
Company is requested for the Season.

"JOHN M. SCOTT, THOMAS CADWALADER, JOSEPH SWIFT, CHARLES WILLING, RICHARD VAUX, M. G. EVANS,	} <i>Managers.</i> {	JAMES H. BLIGHT, B. W. INGERSOLL, WILLIAM T. TWELLS, ALEXANDER BIDDLE, WILLIAM W. FISHER, BERNARD HENRY, JR."
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During the Civil War the Assemblies were completely stopped ; but after the conclusion of that great struggle they were revived in 1866, at the Academy of Music, by Dr. Alexander Wilcocks, who was a Manager before the war, William Henry Rawle and other gentlemen.

We Americans, in the rush and stress of every-day life, are too apt to forget that those things we enjoy to-day are in a measure due to those who built in an earlier time. It is good to have some reverence for the experiences of the past as we prepare for the future. Charles Lamb, in one of his sonnets, tells us :

"'Tis man's worst deed  
To let the things that have been run to waste,  
And in the unmeaning present sink the past :  
In whose dim glass even now I faintly read  
Old buried forms and faces long ago."

While we should not worship what has been so much as to forget



to labor in the present and for the future, we should not be entirely oblivious of those who have gone before. And as unless old papers and books are properly housed in some collection like that of the American Philosophical Society, they are pretty sure in the changes and ups and downs of fortunes of their various succeeding owners to be eventually destroyed, it is with peculiar pleasure, therefore, that in behalf of my brother, Mr. Edwin Swift Balch and myself, I am able to present to the Society the Account Book of the First Assemblies kept by our great-great-great-uncle, John Swift, and so insure its future preservation.

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*Stated Meeting, May 2, 1902.*

President WISTAR in the Chair.

Present, 7 members.

Mr. Benjamin C. Tilghman, Jr., a newly elected member, was presented to the Chair, and took his seat in the Society.

Letters accepting membership were read from

Mr. Grove K. Gilbert, Washington.

Prof. Paul Haupt, Baltimore.

Prof. Albert A. Michelson, Chicago.

Mr. Benjamin C. Tilghman, Jr., Philadelphia.

M. Gaston Darboux, Paris.

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*Stated Meeting, May 16, 1902.*

President WISTAR in the Chair.

Present, 19 members.

Prof. Hermann Collitz and Prof. Felix E. Schelling, newly elected members, were presented to the Chair, and took their seats in the Society.

Letters accepting membership were read from

M. Henri Becquerel, Paris.

Prof. G. Johnstone Stoney, London.

A letter was read from the Comité de l'Exposition International de l'Art et de la Paix, inviting the Society to participate in the International Exposition, to be held at Lisbon in May, on the anniversary of the Conference at The Hague.

The decease was announced of

Mr. Paul Leicester Ford, at New York, on May 8, aged 37.

President Henry Morton at Hoboken, on May 9, aged 65.

Mr. Stewart Culin read a paper on the Indians of the Southwestern United States.



PROCEEDINGS  
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THE GEOGRAPHICAL DISTRIBUTION OF FRESHWATER  
DECAPODS AND ITS BEARING UPON  
ANCIENT GEOGRAPHY.

BY DR. A. E. ORTMANN.

*(Read April 3, 1902.)*

INTRODUCTION.

During the last decennium Zoogeography has developed in a very peculiar direction, which, in a large part, is directly opposite to the methods introduced by Wallace. The professed aim of the latter was the creation of a zoogeographical division of the earth's surface into regions, realms and the like, the purpose of which was the subordination of the facts of animal distribution under a fixed scheme; and since it was self-evident from the beginning that the distribution of animals ought to express the physical conditions of the earth's surface, it was assumed that the proposed zoogeographical divisions correspond to the chief features of the distribution of the conditions of life.

Soon, however, it was discovered that it is impossible to give a division of the earth's surface that could claim general recognition. It is true that each of the proposed schemes was actually supported by more or less numerous instances of distribution, and that in many cases the physical factors influencing and explaining these divisions were easily understood; but there was always alongside of the supposed normal conditions a number of exceptional cases, where the actual distribution of certain animals or animal groups was directly the opposite. One of the chief causes of this fact has already been recognized and carefully studied by Wallace. It is

the difference of the means of dispersal of the various groups of animals. On account of these anomalies Wallace constructed his regions chiefly for Mammals and Birds, excluding all the rest of the animal kingdom.<sup>1</sup>

This method, however, can never be satisfactory. It amounts to nothing but the creation of an arbitrary scheme which may correspond to some of the facts; but if there are any other facts that do not fit into it—as very often happens—they are simply thrown out and neglected.

But this is not all. Even the restriction of Wallace's regions to a single group of animals proved insufficient to cover all cases within this group. This is true also of all other schemes that have been proposed by other writers for the same or other smaller groups. In every single instance there were exceptions to the rule, and for some time it seemed difficult or even impossible to deal with these apparent anomalies; in fact, none of the proposed divisions into regions can be applied to all cases, even within smaller groups.

The correct understanding of this fact, that a large number of animals does not submit to any of the proposed schemes that profess to comply with the present distribution of the condition of life, was made possible by the consideration that the actual distribution of any animal must have originated in the past. Although there are some animals the history of which does not go very far back, in a geological sense, there are others which do, and, generally speaking, we may say that the farther back we go in geological history the more different were the conditions of life from what they are now, and the present distribution of the respective forms must necessarily appear the more strange and anomalous. Wallace, indeed, tried to remove this difficulty in a very peculiar way. He simply propounded his principle of the permanency of the continents, which means to say that the present distribution of land and water (and in general of the physical conditions of life) did not change materially during the earth's history, and that the external features of the earth's surface have remained practically identical from time immemorial up to the present. That this principle is without

<sup>1</sup> This exclusive restriction to the higher forms of life (Mammals, Birds) is a principle of Wallace and has been expressly maintained by him as late as in 1894 (see *Nature*, Vol. xlix, 1894, p. 610).

proper foundation has now been recognized and the opposite opinion begins to prevail, that abnormal conditions of distribution are due to just such changes of the physical conditions during a geological past, and that cases of this kind may often enable us to draw conclusions as to the reconstruction of the old conditions. We may safely assume that the character of the physical conditions of the earth's surface has changed continuously and variously in the past and that we possess among living animals many forms which express in their present distribution not only the Tertiary state, but which may also represent Mesozoic or even Palæozoic conditions. Thus it is evident that investigation of the present distribution cannot be used as the starting point for the construction of any scheme. This has been done, however, not only by Wallace—who entirely disregarded the above fact—but also by others, who paid due attention to it. Indeed Osborn<sup>1</sup> has pronounced it the purpose of Zoogeography to unite past and present distribution into one scheme, and the same idea has led Jacobi<sup>2</sup> to attempt practically this union.

But if we study the most prominent differences between past and present we see that they are chiefly found in the different distribution of land and water, and that frequently in past times land connections existed between parts which are now separated, or *vice versa*; and thus it is self-evident that the solution of Osborn's problem is simply impossible, since there is no way to express separation and connection of the identical parts in one and the same scheme.<sup>3</sup>

We consequently arrive at the following three conclusions:

1. *Any division of the earth's surface into zoogeographical regions which starts exclusively from the present distribution of animals, without considering its origin, must be unsatisfactory, since always only certain cases can be taken in while others remain outside of this scheme.*

2. *Considering the geological development of the distribution of*

<sup>1</sup> H. F. Osborn, "The Geological and Faunal Relation of Europe and America During the Tertiary Period, etc.," in *Ann. N. Y. Acad. Sci.*, Vol. xiii, 1900, p. 48, and in *Science*, April 13, 1900, p. 563.

<sup>2</sup> A. Jacobi, "Lage und Form biogeographischer Gebiete" (*Zeitschr. Ges. fuer Erdkunde*, Berlin, Vol. xxxv, 1900).

<sup>3</sup> This, of course, does not dispose entirely of Osborn's problem. On the contrary, it remains "the" problem of Zoogeography, only we have to change its formal expression and to say that the *historical union* of past and present distribution is the purpose of zoogeographical study.

*animals, we must pronounce it impossible to create any scheme whatever that covers all cases.*

*3. Under these circumstances it is incorrect to regard the creation of a scheme of animal distribution as an important feature or purpose of zoogeographical research.*

Thus we are justified in saying that zoogeographical study, as introduced by Wallace, is not directed in the proper channels, and we are confronted with the question, If the creation of regions of animal distribution is not a matter of first importance, which is the vital point in this branch of research?

This question has been practically answered by many writers. I name the following: G. Pfeffer, E. von Ihering, H. A. Pilsbry, R. F. Scharff, C. Hedley, W. Kobelt, H. F. Osborn, A. Jacobi (besides others), and these we may take as representatives of the modern tendency in Zoogeography. According to these authors the chief aim of zoogeographical study consists—as in any other branch of biology—in the demonstration of its geological development. We have to designate this most emphatically, as the final goal of Zoogeography: the retracing of the present animal distribution to its beginning in the past, and a corollary of this is the reconstruction of the ancient physical features of the earth's surface, since these in the first place have guided the development. In the latter respect the distribution of land and water in past times is all-important and the easiest to be traced.

Thus Zoogeography becomes a very important aid not only to physical Geography itself, but also to historic Geology.

The above introductory remarks seem necessary, because the purpose and methods of the new tendency in Zoogeography have been frequently misunderstood, and especially because it was not seen that in this way the fruitless discussions on the limits and value of the different zoogeographical regions, etc., have been rendered unnecessary. Yet it is a habit among zoogeographers to create or discuss zoogeographical regions according to Wallace's ideas, and this is done not only by writers who, like Wallace and Sclater, are principally opposed to any progress in Zoogeography, but also by those who are familiar with the new ideas about the geological development of animal distribution. The old method has become an integral part of this branch of science to such a degree

that any research in this direction is deemed incomplete that is not finished by the creation or discussion of "regions."

In opposition to this, we wish to emphasize that we consider it entirely a matter of indifference whether we accept any regions or not, since none of the possible schemes can be satisfactory. Only in a very limited degree and in a modified sense we believe it advisable to divide the earth into regions, and we have proposed such a division for the marine life districts.<sup>1</sup> This scheme, however, is not intended to represent or to express the actual distribution of any animals, but it is a scheme of the distribution of the conditions of existence in the oceans of the present time without consideration of the past or of any definite group of animals. The only purpose of these regions is to single out those marine animals which correspond to the normal conditions of life and to separate them from the abnormal cases; under "*normally distributed*," consequently, we mean those animals which shape their distribution according to the present features of the earth's surface and which belong in their origin to recent time. All the rest differs and does not fit into these regions; but instead of leaving them out of consideration we know that just these cases are the most interesting, since they demand closer investigation. In most cases we find that these instances of "abnormal" distribution are to be traced back into the geological past in order to be properly understood. This latter study is the most important branch of Zoogeography, and we see that the introduction of "regions" in our method is only the means by which we discover the more interesting and important cases, but it is not the final aim.

Of course the same method may also be used for land and fresh-water animals, and it may here be incidentally remarked that the regions proposed by Wallace are in this respect superior to any modifications introduced by later authors, since they generally are well limited and isolated by physical boundaries given on the surface of the earth. But if we are satisfied with the simple statement of the fact that some animals fit into these regions while others do not, we do not approach the solution of the question as to how the actual distribution originated: we are to advance one step further and investigate those cases which do not submit to the scheme. The final aim of this investigation is to compare and group together

<sup>1</sup> Ortman, A. E., *Grundzuge der marinen Tiergeographie*, Jena, 1896.



those abnormal cases which resemble each other. Thus we gain certain general views as to ancient geography, and we are finally enabled to trace the distribution of land and water, of climatic conditions and the like in the geological past.

Most prominent among the groups of animals that are available for these investigations are the *Mammals*, and they have actually been used for just this purpose by various authors (Doederlein, Zittel, Lydekker, Scharff, Osborn). The palæontological material within this group is the most complete of all. But there is one important drawback: since the history of the *Mammals* hardly goes back beyond Tertiary times, at any rate since the palæontological record of this group is more or less complete only within the Tertiary, we can only draw conclusions from them as to the geographical conditions of this period, while we have to refrain from an investigation of those of the Mesozoic times.

This is a very different matter with the land and freshwater *Mollusks*. According to what we know, it is apparent that many of these forms can be traced back to Mesozoic times, sometimes even to Palæozoic, and, indeed, it is this group of animals that has furnished the material for the studies of von Ihering, Pilsbry, Hedley, Kobelt, and we are to expect that further investigation in this direction may yield interesting results.

Other groups have also been used. Von Ihering introduced the study of *Ants*, and there may be other promising groups among the *Insects* (for instance *Spiders*). But since the majority of the *Insects* possess unusual means of dispersal (power of flight) that are apt to obscure the original conditions of distribution, *Insects* in general are not well adapted to this kind of research. Of other animals the *Earthworms* have been studied in this respect (by Beddard), and of the Vertebrates, *Reptiles*, *Amphibians*, and freshwater *Fishes* are very likely to prove good objects, since their history in many cases goes back to the beginning of the Mesozoic or even to the Palæozoic time.

In the following treatise I wish to call special attention to certain groups of *Decapod Crustaceans* that live in fresh water. In part these have been discussed previously by other writers as well as by myself, but it is worth while to go more into detail, since we shall find them very interesting in this respect.

The following groups of freshwater Decapods are known :

FAMILY: *Atyida*.

*Palæmonida* (in part).

*Potamobiida*.

*Parastacida*.

*Ægleida* (monotypic).

*Potamonida*.

There are, scattered among other families, other forms of freshwater Decapods, but the above are the most important groups. These are found either exclusively in fresh water or possess the largest number of their members there, and are found only in rare cases in the sea.

As regards the *Atyida*, the present writer has collected the chorological material in a previous paper.<sup>1</sup> This is no doubt one of the oldest groups of freshwater Decapods, and their origin, as is very likely also according to their morphological characters, is to be sought for possibly in Jurassic times, although fossil forms are not positively known. The chief features of their distribution are excessively abnormal and even confusing, and therefore the extreme age of the group is again confirmed. On the other hand, there are smaller groups within this family, the distribution of which was apparently formed in later times. Since there is every reason to believe that our knowledge of the actual distribution of the *Atyida* is still more or less defective, we shall refrain from discussing it and refer only to the latest summary given by the present writer.<sup>2</sup>

In the family of the *Palæmonida* the genus *Palæmon* forms a group that possesses numerous species which are found chiefly in fresh water. Their distribution, which has also been previously investigated by the present writer,<sup>3</sup> points distinctly to the fact that this genus is a very recent one, which is at the present time just in the act of immigrating into fresh water, and that this process is by no means completed. The different species depend in their dis-

<sup>1</sup> Compare Ortmann, A. E., in Bronn's *Klassen und Ordnungen des Tierreichs*, Vol. v, 2, 1899, p. 1185. We leave out of consideration the families *Canobitida* and *Gecarcinida*, which are more properly land animals. See *ibid.*, pp. 1183 and 1184.

<sup>2</sup> Ortmann, in *Proc. Acad. Philadelphia*, 1894, p. 397 ff.

<sup>3</sup> In Bronn's *Klassen und Ordn.*, l. c., 1901, p. 1286 f.

<sup>4</sup> In *Zool. Jahrb. Syst.*, Vol. v, 1891, pp. 744-748, and in Bronn's *Klassen und Ordn.*, l. c., 1901, p. 1291 f.

tribution largely on the conditions prevailing in the littoral waters, and generally they follow the physical regions which we have proposed for the marine littoral district of the present time. To this there are only a few exceptions, due to special means of dispersal (crossing over continental divides, for instance). For the investigation of ancient Geography this genus has no value.<sup>1</sup>

In the following we shall treat of the remaining four families: *Potamobiidæ*, *Parastacidæ*, *Ægleidæ* and *Potamonidæ*.

## PART I. CHOROLOGICAL MATERIAL.

### A. CHOROLOGY OF THE FAMILIES POTAMOBIIDÆ AND PARASTACIDÆ. (See Fig. 1.)

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##### (a) General Discussions and Systematic Revisions.

HUXLEY, TH.: *The Crayfish*, London, 1879.

FAXON, W.: "A Revision of the Astacidæ" (*Mem. Mus. Harvard*, Vol. 10, 1885).

<sup>1</sup> Coutière, H. ("Sur quelques Macrures des eaux douces de Madagascar," in *C. R. Acad. Sci. Paris*, Vol. cxxx, 1900, pp. 1266-1268), discussing the *Palæmons* of Madagascar, has advanced some views as to their distribution and concludes by putting the (unanswered) question whether this distribution has formed under conditions similar to the present ones or not. This question, however, has been answered in detail by the present writer in the paper quoted above (1891), with which Coutière seems to have been unacquainted. This is also evidenced by the fact that some of the peculiarities of distribution in this genus, emphasized by the present writer, are not mentioned by Coutière—for instance, the relation of the West African species to those of America. Coutière holds that the West African (not South African) *Palæmon vollenhovens* Herkl. is most closely allied to *P. brevicarpus* Haan from Japan, while I regard the relationship to the American *P. jamaicensis* (Hbst.) as more important.

As regards *Bithynis hildebrandti* Hlgdf. (1893) from Madagascar, I believe it is hardly possible to connect this species genetically with the type species of this genus from Chile. I think this is a case of convergency. The opinion of Coutière, that the theory of a Posttriassic connection of Madagascar with India and Africa is to be abandoned, has no support whatever. The distribution of *Palæmon*, which, according to Coutière himself, does not go back beyond Miocene times, is absolutely irrelevant to this question, and even the Miocene age of *Palæmon* seems to be doubtful. The presence of identical species on the eastern and western sides of the Cordilleras in South America is no evidence for this, since this distribution is not discontinuous, and the respective species have apparently crossed this chain of mountains, and are actually found in the mountains high up in the headwaters of the Anazonas river, for instance.



FIG. 1. Distribution of the Crayfishes of the families *Potamobidae* and *Parastacidae*.

- FAXON, W.: "Notes on North American Crayfishes, Family Astacidae" (*Pr. U. S. Mus.*, Vol. 12, 1890).
- FAXON, W.: "Observations on the Astacidae in the U. S. National Museum and in the Museum of Comparative Zoology, with Descriptions of New Species" (*Pr. U. S. Mus.*, Vol. 20, 1898).
- ORTMANN, A. E.: "Ueber Bipolarität in der Verbreitung mariner Thiere" (*Zool. Jahrb. Syst.*, Vol. 9, 1896, p. 588-594).
- ORTMANN, A. E., in Bronn's *Klassen und Ordnungen des Thierreichs*, Vol. 5, Part 2, 1901, pp. 1288-1290.

(b) *Special Literature, published after Faxon's Revisions (1885, 1890, 1898), or not embodied in them.*

- BERG, C.: "Datos sobre algunos crustaceos nuevos para la fauna argentina" (*Commun. Mus. Buenos Aires*, Vol. 1, 1900).
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- PHILIPPI, R. A.: (Descriptions of Three Species of Crayfishes from Chile) (*Annales Univers. Chile*, Vol. 61, 1882, pp. 624-628, with plate).<sup>1</sup>
- PHILIPPI, R. A.: "Dos palabras sobre la sinonimia de los Crustaceos, Decapodos, Braquiuros o jaivas de Chile" (*Ann. Univers. Chile*, 1894).

For the intended publication of the Decapods in the "Thierreich," edited by the German Zoological Society, the present writer was obliged to make a complete collection and a critical review of the systematic literature of these two families. Of course, the results of these studies are embodied in the following portion of this article, although it is not possible to refer to this work, the manuscript of which has just been finished.

1. Family: POTAMOBIIDÆ Huxl.<sup>2</sup>

The family *Potamobiidae* is divided into two genera: *Potamobius* Sam. and *Cambarus* Er. The latter is no doubt the more special-

<sup>1</sup> Of this rare paper I possess a handwritten copy and sketches of the figures, through the kindness of Dr. F. Philippi, of Santiago.

<sup>2</sup> Those authors (Faxon, Rathbun) who retain for the European crayfish the

ized one, and its distribution is more sharply limited than that of *Potamobius*, it being found only in the eastern parts of North America, Mexico and Cuba.

Genus: *Cambarus* Er.

The genus *Cambarus* contains at present sixty-six well-known species; of a sixty-seventh, the group to which it belongs is doubtful (*C. clypeatus* Hay, Missouri). The species form five groups within the genus.

Sixteen species belong to the first group, namely:

- |                               |                                 |
|-------------------------------|---------------------------------|
| 1. <i>blandingi</i> (Harl.).  | 9. <i>versutus</i> Hag.         |
| 2. <i>hayi</i> Fax.           | 10. <i>spiculifer</i> (Lec.).   |
| 3. <i>fallax</i> Hag.         | 11. <i>pellucidus</i> (Tell.).  |
| 4. <i>clarki</i> Gir.         | 12. <i>acherontis</i> Loennb.   |
| 5. <i>troglodytes</i> (Lec.). | 13. <i>wiegmanni</i> Er.        |
| 6. <i>lecontei</i> Hag.       | 14. <i>allemi</i> Fax.          |
| 7. <i>angustatus</i> (Lec.).  | 15. <i>evermanni</i> Fax.       |
| 8. <i>pubescens</i> Fax.      | 16. <i>penicillatus</i> (Lec.). |

Eight species belong to the second group:

- |                          |                                    |
|--------------------------|------------------------------------|
| 1. <i>cubensis</i> Er.   | 5. <i>gallinus</i> Cock. and Port. |
| 2. <i>carinatus</i> Fax. | 6. <i>gracilis</i> Bund.           |
| 3. <i>mexicanus</i> Er.  | 7. <i>carolinus</i> Er.            |
| 4. <i>simulans</i> Fax.  | 8. <i>advena</i> (Lec.).           |

To this group possibly belongs *clypeatus* Hay.

Thirteen species belong to the third group:

- |                             |                                     |
|-----------------------------|-------------------------------------|
| 1. <i>acuminatus</i> Fax.   | 8. <i>uhleri</i> Fax.               |
| 2. <i>bartoni</i> (Fabr.).  | 9. <i>setosus</i> Fax.              |
| 3. <i>longulus</i> Gir.     | 10. <i>extraneus</i> Hag.           |
| 4. <i>latimanus</i> (Lec.). | 11. <i>jordani</i> Fax.             |
| 5. <i>dubius</i> Fax        | 12. <i>cornutus</i> Fax.            |
| 6. <i>diogenes</i> Gir.     | 13. <i>hamulatus</i> Cope and Pack. |
| 7. <i>argillicola</i> Fax.  |                                     |

generic name of *Astacus* M. E., claim that Latreille (Consider. génér., etc., 1810; see Faxon, 1898, p. 662) has made this species, *Astacus fluviatilis* Fabr., the type of the genus *Astacus* Fabr. This statement of Latreille, however, is erroneous, since *Astacus* of Fabricius is a genus without type, and remained such until Samouelle (*The Entomologists' Useful Compendium*, 1819, p. 95) separated *Astacus* and *Potamobius* (Lobster and Crayfish). See Faxon, 1885; Ortmann, "Das System der Decapodon Krebse" (*Zool. Jahrb. Syst.*, Vol. 9, 1896, p. 430), and Stebbing (in *Natural Science*, Vol. 12, 1898, p. 239 ff.).

Twenty-six species belong to the fourth group :

- |                                 |                               |
|---------------------------------|-------------------------------|
| 1. <i>mississippiensis</i> Fax. | 14. <i>virilis</i> Hag.       |
| 2. <i>immunis</i> Hag.          | 15. <i>nais</i> Fax.          |
| 3. <i>medius</i> Fax.           | 16. <i>pilosus</i> Hay.       |
| 4. <i>lancifer</i> Hag.         | 17. <i>longidigitus</i> Fax.  |
| 5. <i>palmeri</i> Fax.          | 18. <i>sloanei</i> Bund.      |
| 6. <i>difficilis</i> Fax.       | 19. <i>rusticus</i> Gir.      |
| 7. <i>alabamensis</i> Fax.      | 20. <i>meeki</i> Fax.         |
| 8. <i>compressus</i> Fax.       | 21. <i>harrisoni</i> Fax.     |
| 9. <i>propinquus</i> Gir.       | 22. <i>forceps</i> Fax.       |
| 10. <i>neglectus</i> Fax.       | 23. <i>spinosus</i> Bund.     |
| 11. <i>digueti</i> Bouv.        | 24. <i>erichsonianus</i> Fax. |
| 12. <i>affinis</i> (Say).       | 25. <i>putnami</i> Fax.       |
| 13. <i>indianensis</i> Hay.     | 26. <i>hylas</i> Fax.         |

Three species belong to the fifth group :

- |                            |                          |
|----------------------------|--------------------------|
| 1. <i>montezumæ</i> Sauss. | 3. <i>shufeldti</i> Fax. |
| 2. <i>chapalanus</i> Fax.  |                          |

In discussing the distribution, it is best we take up the single groups. The species of the *first group* are restricted chiefly to the southern parts of the United States and Mexico, and we observe that all, with two exceptions (*blandingi* and *pellucidus*), are found in the region of North America formed by Mexico, Texas, Louisiana, Mississippi, Alabama, Florida, Georgia and South Carolina. *C. blandingi* possesses the widest range ; in the States named it is wanting only in the farthest southeast, in Florida and Georgia<sup>1</sup>; but on the other side it extends beyond those limits along the Atlantic coast, passing through North Carolina, Maryland and New Jersey into the neighborhood of New York, and in the Mississippi-Ohio basin it extends northward through Arkansas, Tennessee, Missouri, Illinois and Indiana into Ohio and southern and eastern Iowa. Westward, it has been found as far as Indian Territory. *C. pellucidus* is a blind cave species which is restricted to certain localities in Indiana and Kentucky.

It is apparent that the centre of this group is in the Gulf States and in the southern Atlantic States, while the region of the eastern mountains (Allegheny system) is left unoccupied by it, and only one species advances northward along the Atlantic coast and in the

<sup>1</sup> It is very likely to be discovered in Georgia.

Mississippi valley to the neighborhood of the Great Lakes. To this latter extension of the range also belongs *C. pellucidus*. Southward, this group goes through Texas (here it has been found near the Mexican boundary line), and is found in the neighborhood of the city of Mexico (*C. wiegmanni*). Whether this latter locality is connected with the localities in Texas or not is unknown.

The centre of distribution of the *second group* is to be found in the Southwest. We know two species from Mexico, two from New Mexico, Texas and Kansas. Another species (*C. gracilis*) extends from these parts northward (in the prairies), and is found in Kansas, Iowa, Illinois, as far as Wisconsin. In the South we have, more or less isolated, *C. clypeatus* in Mississippi, and absolutely isolated are *C. carolinus* and *advena* in South Carolina and Georgia and *C. cubensis* in Cuba.

Within this group we observe a very striking *discontinuity*; not only the Mexican localities are separated from those in the United States, but also in the Gulf States, the southern Atlantic States and in Cuba there are representatives of this group, separated from the rest in the Southwestern and Central States.

Very different is the range of the *third group*. Here we have complete continuity, and the centre is evidently in the system of the Allegheny mountains and in the East. The species are very numerous in the mountainous parts of Tennessee, Kentucky, North Carolina, Virginia and West Virginia, Maryland, Pennsylvania, and in the adjoining parts of Ohio and Indiana. This group is also well represented in Illinois, and extends, gradually decreasing in density, westward into Wisconsin, Minnesota, Iowa, Missouri (in the eastern part only), Arkansas and the Indian Territory. It is very rare in Texas, Louisiana, Mississippi; is slightly represented in Alabama, Georgia and South Carolina, but is wanting in Florida. In a northeasterly direction, a single species (*C. bartoni*) extends over New York and New England across the Canadian boundary into New Brunswick, where it reaches the Restigouche river, a tributary of the Gulf of St. Lawrence. The same species is found in the northern affluents of Lake Ontario (Toronto) and the St. Lawrence river in Quebec (St. John's Lake), where it marks the northern boundary of the genus. In Michigan this group is represented in the neighborhood of Lake Huron, but it has not been found north of the Great Lakes in Canada. The northeastern extension of the range of this group, on the one hand, is very



the Upper Jurassic (Neumayr, 1890, p. 329), which reach the Pacific Ocean. Beds of the same age are known on the Aleutian Islands and in Alaska. These deposits exhibit a peculiar character, which has been called the boreal or arctic type, and in this respect the Jurassic beds of the western coast of North America are very important, since they agree with the boreal type. Neumayr concluded from this that the Upper Jurassic Polar Sea sent an extension southward along the western coast of North America into the North Pacific, and its fauna also extends in this direction; by this extension of the Polar Sea, east Asia was separated from North America. Consequently there was no land bridge.<sup>1</sup>

These conditions of Upper Jurassic times continued, according to Neumayr, into the Lower Cretaceous; the Wolga-stage, with its characteristic Aucella-beds, belongs in part to the Lower Cretaceous, and the Polar basin was also in the beginning of the Cretaceous in open communication with the northern Pacific. This is represented in Koken's map (1893, pl. 1), although Asia and North America approach each other considerably. This same map, however, expresses, for the Upper Cretaceous, a separation of the Polar Sea from the Pacific, and this land connection between Asia and North America is preserved in Koken's map for the older Tertiary (*l. c.*, pl. 2). The evidence for this disconnection of the oceans in the Upper Cretaceous time is given by Neumayr (1890, p. 389-391); palæontologically, we can trace a continuous Upper Cretaceous ocean, including the northern Pacific from California to Japan, which was connected with south India. This province differs strikingly from the American-European (Atlantic) province; the Polar Sea was much reduced in size, and, to all appearances, Siberia was largely dry land and was connected with North America.

Thus there is some evidence of the existence of a land connection between Siberia and Alaska, beginning at about the middle of the Cretaceous period, and continuing up to the end of the Tertiary. Whether this connection was continuous in time, or interrupted at certain periods, is hard to decide; at all events, it was of such a character that an easy and free communication was possible between the respective parts, and this is expressed very distinctly in the faunas of the northern land masses, although the

<sup>1</sup> This Jurassic ocean forms apparently the continuation of the old Triassic basin, comprising the Pacific and Arctic Oceans (see Neumayr, p. 266).

Taking together the distribution of the five groups, we find that the range of the genus *Cambarus* extends over the following parts of North America: In Mexico, the respective species are reported from the following States: Vera Cruz (near Vera Cruz and Orizaba), Pueblo, Mexico, Michoacan. This line would represent the southern boundary of the range.<sup>1</sup> Further, the genus has been found in the States of Jalisco and Sinaloa (Mazatlan) (in the drainage of the Pacific Ocean); on the central plateau, in Guanajuato, San Luis Potosi (Santa Maria) and Coahuila (Parras). This latter locality forms in a certain degree the connection of the Mexican part of the range of the genus with that of the United States, since the Mexican State Coahuila extends northward to the Rio Grande del Norte, and just across this river, on its left bank, there is, in Kinney county, Texas, a locality for *C. clarki*. Thence the range of the genus is apparently continuous, and reaches eastward to the sea (Gulf of Mexico and Atlantic Ocean).<sup>2</sup> Toward the west and north it is circumscribed by the following line: from Kinney county, Texas, to New Mexico (including its eastern part), then receding toward Indian Territory and leaving out Oklahoma, farther, including Kansas, the southeastern corner of Wyoming (possibly a part of Colorado), the southern and eastern part of Nebraska, crossing here the Missouri, including Iowa and Minnesota and possibly parts of the Dakotas, at any rate the northeastern corner of North Dakota, crossing over into Canadian territory and including the region of Lake Winnipeg and Saskatchewan river (northernmost point). Thence this line recedes in a southeasterly direction, reaches Lake Superior, and follows the Great Lakes as far as Lake Erie. At Lake Ontario it advances again northward and follows at a certain distance the St. Lawrence river, reaching at the Lake St. John in Quebec the northernmost point in the East. Then it turns southward, crosses the St. Lawrence and includes, in New Brunswick, the drainage of the Restigouche and Miramichi rivers (emptying in the St. Lawrence Gulf) and also the St. John river (emptying in the Bay of Fundy). Thus the largest part of New Brunswick seems to belong to the range of this genus, while

<sup>1</sup> The genus is said to be represented near Alta Vera Paz, in Guatemala (Faxon, 1885, p. 173). This would advance the range southward beyond the Isthmus of Tehuantepec. This locality, however, needs confirmation.

<sup>2</sup> In Florida, only in the northern half are localities known, southward as far as Orange, Lake and Hillsboro counties.

Australian fauna is derived from Asia (see von Ihering, 1894, p. 406, and Hedley, 1899).

This connection between east Asia and Australia (Sino-Australian) is not well expressed in Jacobi's scheme. The apparent reason for this is that Jacobi considered chiefly those groups of animals (Mammals, Birds) which do not bear upon this question. Nevertheless, some of his "regions of dispersal" come under this head, namely, the ninth, tenth, eleventh and twelfth (Papuan, Farther Indian, Philippine, southern Japanese; see Jacobi, 1900, pp. 208-210), and discussing the Papuan, he directly mentions the Oriental origin of certain elements of it, thus indicating its relation to southeastern Asia.

Studying the tectonic configuration of the repective parts, we are to remember that Australia belongs to the old, Palæozoic Gondwana land of Suess (1888, p. 317 ff.), which also comprised Africa and India. But we cannot refer to this old connection of Australia with India, since India in turn was not then united with the rest of Asia, and since this connection was destroyed in very early times, possibly in Palæozoic. For a tectonic connection of Australia and eastern Asia (excluding India) we have only evidence to the contrary.

On the other side, the eastern parts of present Asia, especially China, northeastern Siberia, and Farther India, form a more or less complete tectonic unit. Suess (1888, pp. 206-242) has shown that this whole region consists largely of old archaic and palæozoic rocks, which form, in northern China, an old continental mass, in the south a series of folded mountain ranges (p. 287), which continue into the mountains of Tonkin and Anam as far as the mouth of the river Mekong. In this whole region no Mesozoic deposits (with the exception of Rhætic beds in Tonkin) are known. According to Koken,<sup>1</sup> a Triassic ocean extended from the region of the Himalaya mountains and Central Asia to the shores of the present Pacific, covering a large part of China. The latter may have been land before Rhætic times; but at present we have only evidence that it was surely land in the Jurassic period.<sup>2</sup>

<sup>1</sup> *Neues Jahrb. f. Mineral.*, etc., 1900, Vol. 1, p. 196.

<sup>2</sup> See Loczy, L. von, *Wissenschaftliche Ergebnisse der Reise des Grafen Bela Szechenyi in Ostasien*, Vol. 3, 1899; the Central-Chinese sea (south of the Kuen-Lun mountains) disappeared at the end of Triassic and in Jurassic times.

As regards the morphological relations of the five groups, we are to consider first Faxon's view (1885, p. 19), that the species of the first group are morphologically the most primitive ones. He draws this conclusion chiefly from the shape of the male copulatory organs. If we compare, however, certain species of the second group (*simulans*, *mexicanus*, *cubensis*) with those of the first group in this respect, we see that they chiefly differ from the latter only in the smaller number of hooks on the pereopoda of the male (only on the third pair, not on the third and fourth, as in the first group). On this account I should prefer to regard the species named as the most primitive forms of the genus, although, on the other hand, I agree with Faxon (1885, p. 47) in believing that the other species of the second group more nearly approach the third group. That the third and fourth groups, compared with the others, are more advanced forms is also my opinion. As the most specialized species I regard those of the third group which have acquired burrowing habits (*diogenes*, *argillicola*, *dubius*). The species of the fifth group differ from all the rest in the presence of hooks in the second and third pereopods of the male, and thus I think they represent an early separated side branch. The copulatory organs of the male in this group resemble in certain respects more those of the first and second groups than those of the third and fourth, and the more primitive character of these species is also suggested by the general shape of the body.

Thus we see that the more primitive forms of the first, second and fifth groups belong chiefly to the South and point distinctly to a connection with Mexico, while among the more advanced and specialized forms of the third and fourth groups this latter connection is hardly expressed or not at all. Their origin and main distribution belong to the more northern parts.

*This points to an origin of the genus in the Southwest, and we believe that the genus came from Mexico and immigrated into the United States in a northeasterly direction.*

A few additional distributional facts tend to support this conclusion. It seems that in those groups which possess a large representation in the Southwest the distribution is rather discontinuous. This is most evident with the second group. Now discontinuity in distribution of any animal is very often a sign of the breaking up of a former continuous range by unfavorable physical conditions. In the present case it appears that at a certain time the immigra-

tion of *Cambarus* from Mexico into the United States did not meet with serious obstacles, but that later in the intermediate regions (northern Mexico and Texas) more unfavorable conditions arose which separated the United States more distinctly from Mexico, and this is possibly due to a more decided development of the desert character of these parts. Thus the Mexican representatives of the first, second, fourth and fifth groups became more or less separated from those in the United States, the first and fourth groups developed more abundantly in the United States, while the third originated there, possibly out of the second group, which in these parts did not make any marked progress and was suppressed and restricted to a few more or less isolated stations, probably on account of its primitive character. An interesting light is thrown upon this question by the presence of one species of the second group (*C. cubensis*) in Cuba. This species is closely related to *C. mexicanus* (Pueblo, San Luis Potosi), while it has no closer relations in the United States, and thus its Mexican origin is most distinctly indicated. Therefore we may safely say of the second group that it is a very primitive one and that Mexico, not the United States, is to be taken as its centre of origin.

The character of discontinuity is more or less noticeable also in the southwestern part of the range of the first, fourth and fifth groups. The first possesses an isolated species (*wiegmanni*) in Mexico, and the stations of *C. blandingi* and *clarki* in Texas are very scattered. In the fourth group we have an isolated species (*digueti*) in Mexico (Jalisco), while *C. immunis*, a species found elsewhere in the northern central basin, has been reported from Orizaba, in Mexico.<sup>1</sup> The fifth group has two species in Mexico and, widely separated from them, a third near New Orleans. If we compare with this the northern part of the ranges of the first, third and fourth groups we see everywhere perfect continuity. In every direction from the centre, except toward the Southwest, the intensity of distribution decreases gradually. This is especially true for the first group, the centre of which is in the Southern States, in the directions northward along the Atlantic coast and upward in the Mississippi Valley. In the third group, whose centre is in the Allegheny system, there is a regular decrease in intensity in all directions, and in the fourth group a very regular decrease is

<sup>1</sup> We have to accept this record, however, very cautiously.

noticeable from its centre in the middle Mississippi basin toward the East, North and West.

Thus we are to recognize the fact that the different groups, chiefly the first, third and fourth, express in their distribution a regular, continuous advance in a northeasterly direction. Toward the North and East is continuity, which represents a more recent stage in distribution, while in the opposite direction, toward Southwest, we observe discontinuity, which characterizes generally a more ancient stage. In the second group we have a very remarkable discontinuity, and this group is a comparatively primitive one, and the fifth group, which is also primitive in some degree, is chiefly found in the Southwest.

All the foregoing considerations tend to justify our conclusion that the migration of the genus *Cambarus* into the United States started in the Southwest, on the Mexican plateau, and advanced in a northeasterly direction.

Taking up now the second point to be considered, the question of the origin and the ancestral forms of the genus *Cambarus*, we shall be satisfied—for the present—with the opinion of Faxon (1885, p. 16), which is also that of the present writer, that this genus is the most highly specialized within the family *Potamobiidae*, a corollary of which is that it must have originated from forms of a lower type, which probably corresponded to the genus *Potamobius*; in fact, it is easy to imagine that *Cambarus* is derived directly from *Potamobius* by the suppression of the single posterior pleurobranchia and the high specialization of the copulatory organs. However, before entering into a more detailed discussion of the relation of *Cambarus* and *Potamobius*, we shall give a sketch of the chorology of the latter genus.

#### Genus *Potamobius*.<sup>1</sup>

It is advisable here to go more into detail, since, on the one hand, a synopsis of the more recent publications in this group is desirable, and since, on the other, the number of species in this genus is comparatively small and our knowledge of them excellent. The genus is divided into two subgenera: *Potamobius* sens. strict. Ortm. (*Astacus* sens. strict. Fax.) and *Cambaroides* Fax.

<sup>1</sup> The following facts have not been put together since Faxon's review (1885). I shall use here chiefly the revision of this group which I have prepared for the "Thierreich."

Subgenus *Potamobius*—twelve species :

## European group :

1. *pallipes* (Lereb.). South and West Europe : Central Spain, France, England, Ireland, Southwest Germany, Italy southward to Naples, Dalmatia, Greece.
2. *torrentium* (Schrk.). Central Europe : Switzerland, South Germany, Bohemia.
3. *astacus* (L.). West Russia (northward to Finland), Austria, Germany, Denmark, South Sweden and Norway (possibly introduced), France, southward to Northern Italy.
4. *leptodactylus* (Eschz.). Ponto-Caspian basin : Hungary (Danube, Theiss), South and Central Russia, northward to the White Sea ; in Siberia in the region of the Caspian Sea. Further, in West Siberia in the basin of the rivers Obi and Irtysh, introduced, as reported, but possibly indigenous (see Faxon, 1885, p. 151).
5. *pachypus* (Rthk.). Estuaries of the Black and Caspian Seas.
6. *colchicus* (Kessl.). Transcaucasia (upper Rion river).
7. *kessleri* (Schimk.). Turkestan (Sir Darja).

## American group :

8. *leniusculus* (Dan.). Washington, Oregon (lower Columbia river), California (San Francisco).
9. *trowbridgei* (Stps.). Washington, Oregon (lower Columbia river).
10. *nigrescens* (Stps.). California (San Francisco), Washington, Alaska (Unalaska).
11. *klamathensis* (Stps.). British Columbia (east of Cascade Mountains), Idaho, Washington, Oregon, Northern California (mountain rivers).
12. *gambeli* (Gir.). In the Rocky Mountains : on the Pacific slope in Utah, Idaho, Wyoming and Yellowstone Park ; on the Atlantic slope ; mouth of Yellowstone river (eastern State line of Montana).

Subgenus *Cambaroides*—four species :

1. *schrenki* (Kessl.). Lower river Amur.
2. *dauricus* (Pall.). Upper river Amur.†
3. *japonicus* (Haan). North Japan : Yesso.
4. *similis* (Koelb.). Korea.

β { Generally speaking the range of the genus *Potamobius* exhibits a striking *discontinuity*, which has often been discussed. One group of species occupies a continuous area in *Europe* (and Western Asia); another in *East Asia*; a third in Western *North America*.<sup>1</sup> It has been said that it is another remarkable fact that the American species resemble the European more than they do the East Asiatic, and that the latter more approach *Cambarus*, which idea is expressed by their position in a separate subgenus named *Cambaroides*. But as regards the gills and the general form of the body,<sup>2</sup> *Cambaroides* belongs without question to *Potamobius*. The male copulating organs are as different from those of *Cambarus* as they are from those of the typical species of *Potamobius*, and the only character that points decidedly to *Cambarus* is the presence of copulatory hooks on the ischiopodites of certain peræopods. But also in this respect *Cambaroides* is rather peculiar, since these hooks are found on the second and third pair, which case is represented among *Cambarus* only in the fifth group (containing only three species), while all the rest of the numerous species of this genus possess these hooks either on the third and fourth or only the third pair.

I am of the opinion that the resemblance of *Cambaroides* to *Cambarus* does not express very close blood relationship, but is due to convergency. The development of hooks on the peræopods of the male, which serve, as is now known, the purpose of taking hold of the female in copulation, is easily understood, if we remember the manner in which copulation is performed, and it is also easily intelligible that this device has possibly developed independently in *Cambaroides* and *Cambarus*. The shape of the copulating organs, which shows no doubt in *Cambaroides* a certain similarity to the *Cambarus* type, can be explained in the same way, since it is quite clear that if they are used in the same manner they may

<sup>1</sup> To the latter area belongs an isolated locality of *P. nigrescens* in Alaska. According to Hay (1899) this species is found all along the western coast of North America, from California to Alaska. To my knowledge intermediate localities between Washington and Alaska have not been published.

<sup>2</sup> Faxon (1885, p. 126) calls the shape of the body "subcylindrical," and says that it resembles that of *Cambarus*. I cannot concur with him in this opinion; the form of the carapace in *Cambaroides* is decidedly rather oval, as in *Potamobius*, and besides there are variations also in this respect within the genus *Cambarus*.



assume the same or a similar form. If, finally, Faxon says that the shape of the chelæ in *Cambaroides* resembles those of *Cambarus*, he means apparently only the general weak development of them, and we must bear in mind that many *Cambari* are more like typical *Potamobii* in this respect.<sup>1</sup>

Thus the view seems supported that *Cambaroides* is not so very closely related to *Cambarus*, as has been hitherto supposed, and that the similarities which were emphasized are due only to convergency. If we peruse the comparison of the characters of *Cambaroides*, *Potamobius* and *Cambarus* given by Faxon (1885, pp. 126, 127), we find that *Cambaroides* is in some of them more isolated, and that it resembles in others even more the West American species of *Potamobius*. (For instance, the lack of a transverse suture of the telson; the shape of the second male abdominal appendage; the lack of the first abdominal appendage in the female.)

The conclusion drawn from the foregoing is that in certain respects (telson, second pleopods of male, first pleopods of female) *Cambaroides* represents a type that points to the West American *Potamobii*, while the European species are more divergent from it, and there is nothing that opposes the view that this subgenus (which might as well be regarded as a separate genus) forms the starting point on the one side for the European *Potamobii* and on the other for the American *Potamobii*, while subsequently it has changed itself and become different from both (in the male copulatory organs).

The subgenus *Cambaroides* is restricted to the northeastern parts of Asia (region of Amur river, Korea, North Japan). The exact boundaries of its range have nowhere been located positively, and it is not impossible that in the Siberian and northern Chinese mountains other representatives of it may exist. For the present the area from which species of *Cambaroides* are known is absolutely separated from the European area of *Potamobius*.

As regards the latter, its centre is apparently in Southern and Central Russia. From these parts the different species extend into Western Europe, southward to Central Spain, Middle Italy and Greece, and in Russia one species passes southward across the Caucasus Mountains. Eastward a species is found as far as Turke-

<sup>1</sup> Some other characters of *Cambaroides* indicate that this subgenus differs from *Potamobius* as well as from *Cambarus*, and these are characters which approach it to the crayfishes of the southern hemisphere. Compare below.

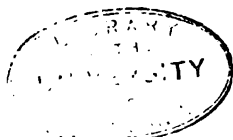
stan, and northward the area reaches the White Sea. East of the Ural Mountains the genus is said to be lacking, but it is found (the widely-distributed species *P. leptodactylus*) introduced in the river Obi and its affluents. Some observations, however, have been made which render it possible that *P. leptodactylus* is an original inhabitant of these parts.

As Huxley (1879) and Faxon (1885, p. 140) believe, the different forms of *Potamobius* have immigrated into Europe from the East, and we can distinguish an older immigration on the part of the group formed by the species *P. pallipes* and *torrentium* and a more recent one on the part of *P. astacus* and its allies. And even within the latter group it seems that *P. astacus* is older than the other species and that it is pushed gradually westward by *P. leptodactylus*, which is spreading in a westerly direction. The writer is of the same opinion, and we shall see below that this is the only theory that is admissible, if we consider the origin of Europe as a continental mass. The occupation of Europe, after it had lost the character of an archipelago and become part of the Eurasiatic continent, was possible for these animals only in a west-easterly direction. This corresponds also to the fact that those forms allied to the European *Potamobii*, which are the nearest geographically, are found to the east of them. They are the forms of *Cambaroides* in Eastern Asia, and we can readily imagine that from the area of distribution of *Cambaroides* an extension existed formerly in a westerly direction across Central Asia, which connected with the European area of *Potamobius*, and this connection represents the direction of the migration.

The forms of *Potamobius* which are found in Western North America possess a continuous area of distribution<sup>1</sup> which is separated from the rest of the genus. Huxley and Faxon, as has been mentioned above, believe that these American species are more closely related to the European, but I think we have reason to accept a different view.

My opinion is that a primitive group, which was ancestral to all three of the living groups, formerly existed in Eastern Asia, which is to be regarded as the centre of origin of the *Potamobiidae*. This group sent out a branch in a westerly direction, which finally reached Europe, and it also sent out a branch in an easterly direction, which migrated apparently along the northern shores of the

<sup>1</sup> Possibly with the exception of the isolated station near Unalaska.



Pacific Ocean and finally immigrated into Northwestern America. A trace of the direction of this route is preserved in the presence of *Potamobius nigrescens* near Unalaska. After the final geographical separation of the European and American descendants from the original group in Eastern Asia each of the three groups developed independently, and the Asiatic group acquired several more advanced characters (copulatory organs and hooks) which otherwise are found only in *Cambarus*, but which do not point to a closer affinity to the latter genus, but are only due to parallelism.

Further, the West American *Potamobii* possess a character that is found also in *Cambarus*. Faxon mentions that the second pleopods of the male resemble not only those of *Cambaroides*, but also those of *Cambarus*, while the European species are different in this respect. This would bring the genus *Cambarus* into closer relation to the West American *Potamobii*, and although this similarity would hardly be of much value by itself, we have to regard it as significant, since it agrees well with the distributional facts. The tracing back of *Cambarus* to *Cambaroides* is geographically impossible, and just this latter difficulty has induced the writer to examine more closely the supposed resemblance of both, and the result is as has been discussed above. A closer connection of the European species of *Potamobius* with *Cambarus* is out of the question,<sup>1</sup> and thus only the third group is left, the West American *Potamobii*.

From the latter group *Cambarus* is very sharply distinguished though and no transitional forms are known. Probably this is due to the fact that the connection of the area of both is far remote geologically—that is to say, that the migration of *Potamobius* into Mexico is very old and that the separation of both genera took place in very early times, the one becoming restricted to Northwestern America (southward to California), the other developing on the Mexican plateau out of the old *Potamobius* stock that originally immigrated thither from the North. Thus the differential characters of *Cambarus* became well fixed and no transitions to the old stock are found any more.

Thus for the family of the *Potamobiidae* we may express the fol-

<sup>1</sup> Faxon (1885, p. 176) thinks that in former times *Cambarus* and *Potamobius* occupied about the same area, and in order to support this he mentions the supposed existence of a blind *Cambarus* in the caves of Carniola, Austria. However, this latter record is entirely erroneous. There exists no *Cambarus* in the caves of Carniola (see Haman, *Europäische Höhlenfauna*, 1896).

lowing opinion as to the origin of its distribution, founded exclusively upon systematic and chorological studies.

The oldest home of the *Potamobiidae* and their centre of origin is somewhere in Eastern Asia. This ancestral stock spread chiefly in two directions: a western extension of the range crossed Central Asia, finally reaching Europe, while an eastern extension went across Bering Strait and reached the western parts of North America. The continuity of this wide area, which was once wholly occupied by the genus *Potamobius*, was interrupted subsequently in Central Asia and where there is now Bering Sea, and thus three isolated areas were formed—in Europe, in Eastern Asia and North-west America. In each one of these parts the genus *Potamobius* continued to develop separately. From the West American stock of *Potamobius* finally issued the genus *Cambarus*, which probably originated in Mexico and thence invaded the central and eastern parts of North America. The origin of *Cambarus* probably lies far back in time, since it shows no marked special affinities to any of the three groups of *Potamobius*, and probably it was separated from the latter genus before it was divided up into those three groups.

## 2. Family *Parastacidae* Huxl.

A systematic revision of this family has not been published hitherto. The present writer has tried to collect the necessary data for a review in the "Thierreich," and although it is not possible to give a complete synopsis, based upon careful criticism of the existing descriptions as well as upon actual specimens, he has obtained a fair general idea of the various forms which make up this family.

According to these studies the present state of our knowledge of the distribution of this group is the following:

### 1. Genus *Cheraps* Er. em. Huxl.

#### Species:

1. *quinquecarinatus* (Gr.). West Australia: Swan river.
2. *quadricarinatus* Mrts. North Australia: Cape York.
3. *bicarinatus* (Gr.). North and East Australia: Port Essington, Cape York, Rockhampton, Burnett river, Sydney, Melbourne, Murray river.
4. *preissi* Er. Southeast Australia: Victoria.

Doubtful species: *australiensis* (M.-E.). Sydney.<sup>1</sup>

2. Genus *Astacopsis* Huxl.

Species:

1. *franklini* (Gr.). N. S. Wales and Tasmania.
2. *serratus* (Shaw). N. S. Wales: Murray river, Murrumbidgee river, Richmond river, Brisbane Water and Paramatta river near Sydney.

The following species represent probably young stages of *A. serratus*: *paramattensis* Bate and *sydneyensis* Bate, both from Sydney.

Doubtful species: *tasmanicus* Er. Tasmania.

3. Genus *Engæus* Er.

Species:

1. *fossor* Er. Tasmania.
2. *cunicularius* Er. Tasmania.

4. Genus *Paranephrops* White.

Species:

1. *planifrons* White. New Zealand, North Island and northern part of South Island.
2. *zealandicus* (White). New Zealand, South Island: Dunedin, Oamaru (Otago).
3. *setosus* Hutt. New Zealand, South Island: Canterbury.

This genus possibly is also represented in the Fiji Islands (Huxley).

A doubtful genus, which perhaps belongs in this neighborhood, is genus *Astaconephrops* Nobili.

Species:

1. *albertisi* Nobili. Southern New Guinea: Katau.

5. Genus *Parastacus* Huxl.

Species:

1. *pilimanus* (Mrts.). Southern Brazil: Rio Grande do Sul. Northern Argentina: Provinces Corientes, Entrerios, Catamarca.

<sup>1</sup> By Nobili (1899, p. 246) this species is classified with *Astacopsis*, and is recorded from the Island of Sorong, west end of New Guinea. It is very doubtful whether this is correct.

2. *brasilensis* (Mrts.). Southern Brazil: Rio Grande do Sul.
3. *hassleri* Fax. Chili: Talcahuano, Tumbez.
4. *defossus* Fax. Uruguay. Brazil: Rio Grande do Sul.<sup>1</sup>
5. *saffordi* Fax. Uruguay. Brazil: Rio Grande do Sul.<sup>1</sup>
6. *varicosus* Fax. Reported from Colima, Mexico.<sup>2</sup>
7. *nicoleti* (Phil.). Chili: Tumbez.
8. *agassini* Fax. Chili: Talcahuano, Llanquihue (Puerto Montt), Tumbez. Argentina: Lake Nahuel Huapi.<sup>3</sup>

Doubtful species: *chilensis* (M.-E.), *spinifrons* (Phil.), *bimaculatus* (Phil.), all three from Chili.

This genus is also found in Sta. Catharina, Southern Brazil, according to Fr. Mueller.

#### 6. Genus *Astacoides* Guér.

Species:

1. *madagascariensis* (M.-E.). Madagascar.

As regards the detailed limits of the range of the single species and genera we are very poorly informed, and, further, it is quite possible that our knowledge of the Australian and South American crayfishes is very incomplete also on the systematic side, and it is very likely that there are many unknown species.

It is evident at the first glance, however, that the distribution of the *Parastacida* is divided into four absolutely isolated areas: Australia (including Tasmania and possibly New Guinea); New Zealand; part of South America; Madagascar. Within each of these areas are peculiar genera: in Australia, *Cheraps*, *Astacopsis*,

<sup>1</sup> I have received these two species, *defossus* and *saffordi*, from Rio Grande do Sul through Dr. H. von Ihering.

<sup>2</sup> This locality most emphatically needs confirmation. It is very surprising that this species has never been rediscovered anywhere in Mexico, although large collections of freshwater Crustaceans from these parts have lately reached the United States Museum.

<sup>3</sup> Through Prof. W. B. Scott, of Princeton, I have received from the La Plata Museum two males and one female of this species from this locality which agree well with the description, with the exception that in the larger (adult) male the right (larger) chela is more elongate, with almost parallel margins, and that the squamiform granules of it are more strongly marked. The smaller male and the female agree perfectly with *P. agassini*.

The lake Nahuel Huapi is situated in the Cordilleras, at the southern extremity of the Argentinian province Neuquen. It drains into the Atlantic through the river Limay Leofu, which finally forms the Rio Negro. This locality is directly east of Llanquihué, in Chili, but on the opposite slope of the Cordilleras.

of *Deckenia* on the Seychelle Islands connects also this group more closely with Africa than with India. Possibly this connection is identical with that over Madagascar, although *Deckenia* has not been found on the latter island.

The presence of *Potamonina* in India, corresponding to the African type (subgenus *Potamonantes*), indicates the full development of the Lemurian peninsula, that is to say, conditions prevailing in the oldest Tertiary, if not earlier. *Potamonina*, represented by forms which resembled the subgenus *Potamonantes*, must have existed at least in the beginning of the Eocene, and their distribution extended over Africa and the Lemurian peninsula, including India. During the Eocene this range was separated into two parts, an African (to which Madagascar belonged) and an Indian, and, beginning in the Miocene, the *Potamonina* had a chance to expand over southern and eastern Asia (Farther India and China<sup>1</sup>). At the same time they availed themselves of the various and changing connections within the region of the Indo-Malaysian archipelago, occupying the latter and reaching Australia. The opening of this region of dispersal offered to this group a new opportunity for a rich development, and the origin of the subgenera *Potamon* and *Geothelphusa* was probably the outcome of it.

We cannot leave this chapter without saying a few words on the Arabian region of dispersal of Jacobi. This extends from north-eastern Africa across Arabia to India. Jacobi mentions the similarity of the Siwalik-fauna of India with the Ethiopian. This, consequently, refers to a very recent period, the later Tertiary. Before this time, in the older Tertiary and in the Mesozoic, this connection is out of question. The *Potamonina*, which, as we have seen, existed in the older Tertiary, show no trace of this connection across Arabia, and, as we shall see below, our knowledge of the ancient geography of these parts is a very fair one. Arabia itself formed originally a part of Africa, and the Red Sea did not exist at all in the earlier Tertiary, it being quite recent (see below). Toward the north, northeast and east Arabia was circum-

<sup>1</sup> There was, possibly, an earlier chance to reach the Sinic continent, in Upper Cretaceous times, and I am inclined to believe that the discontinuous localities of *Potamonantes* (and *Parathelphusa*) in the Indo-Malaysian archipelago point to an immigration of these forms that precedes in time that of *Potamon* sens. strict.

be over India and China, generally over Southern and Eastern Asia. Under this assumption, that crayfishes formerly existed in Southeastern Asia, it also becomes clear by which way the rest of the *Parastacidae* were geographically connected with the *Potamobiidae*, namely, by way of the Indian Archipelago, from the continent of Asia over the Sunda Islands, New Guinea to Australia.

Looking over the various connections between the different isolated areas of distribution of the different groups of crayfishes, which have been suggested by the above chorological and systematical discussions, we may itemize them in the following way:

1. A connection of East Asia with North America by way of Bering Sea.
2. A connection of Cuba with Central America (Mexico).
3. A connection of New Zealand with Australia, possibly over the Fiji Islands and New Guinea.
4. A connection of Australia or New Zealand with South America.
5. A connection of Southeastern Asia with Madagascar and with Australia.

We need further explanation of the following remarkable facts:

1. The absence of *Potamobiidae* in Central Asia.
2. The absence of crayfishes in Southeastern and Eastern Asia.
3. The remarkable geographic restriction and isolation from each other of the crayfishes of the genera *Potamobius* and *Cambarus* in North America.
4. The remarkable boundaries of the area of *Parastacus* in South America.

#### B. CHOROLOGY OF THE FAMILY *ÆGLEIDÆ*<sup>1</sup> (See Fig. 2).

Here we shall leave for the present the crayfishes of the families of the *Potamobiidae* and *Parastacidae* and shall take up the small group formed by the *Ægleidae* of Dana. This seems to be a monotypic family, consisting only of one genus and one species, *Æglea laevis* (Latr.). The following localities are recorded for it:

Chili: Valparaíso, and between Valparaíso and Santiago; Lake Llanquihué, near Puerto Montt.<sup>2</sup> Argentina: Provinces Jujuy

<sup>1</sup> See Ortmann, 1901, p. 1290.

<sup>2</sup> Doffein, *F. SB. Akad. Muenchen*, V. 30, 1900, p. 135.



(this is the northernmost point, near the Bolivian boundary), Tucuman, San Luis,<sup>1</sup> Buenos Ayres.<sup>2</sup> Uruguay. Southern Brazil: Rio Grande do Sul and Santa Catharina.

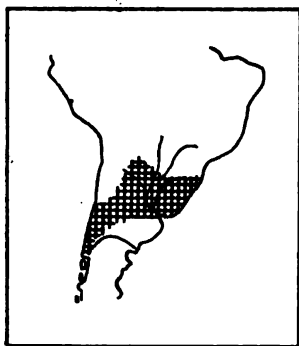


FIG. 2. Distribution of *Aeglea laevis* (Latr.).

As may be seen, the extremities of the range on the Atlantic side, Sta. Catharina and Uruguay, and the southernmost locality in Chili, near Puerto Montt, are also mentioned for the genus *Parastacus*, and in fact the distribution of *Parastacus* and *Aeglea* are almost identical (see figs. 1 and 2), only *Aeglea* seems to extend a little more to the north (Jujuy). This similarity is the more striking, since in both cases the chain of the Cordilleras, which crosses the area of distribution from north to south, has absolutely no effect; both genera are found on either side of this mountain range, and in the case of *Aeglea laevis* and *Parastacus agassizi* the identical species is found east and west of the Cordilleras. This fact is very significant, and important conclusions may be derived from it.

#### C. CHOROLOGY OF THE FRESHWATER CRABS OF THE FAMILY POTAMONIDÆ (See Figures 3 and 4.)

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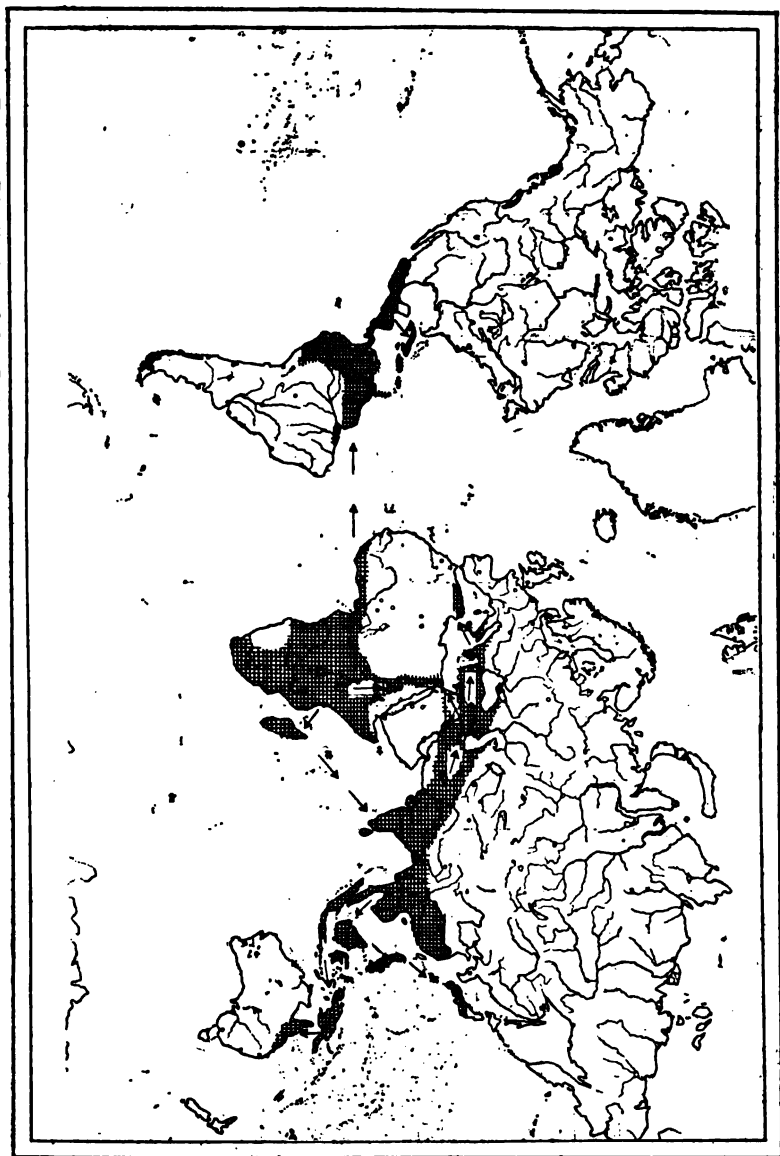
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<sup>1</sup> Nobili, *G. Boll. Mus. Torino*, V. 11, No. 265, 1896.

<sup>2</sup> I have received from the Museum in La Plata specimens that are labeled Ensenada, Rio de la Plata.

FIG. 3. Distribution of the Crabs of the subfamilies *Potamoninae*, *Decapodinae* and *Potamoecarinae*.



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Here a nominal list of the described species of *Potamon*, with localities.

(b) *More recent systematic papers, not included in the above revisions.*

BORRADAILE, L. A.: "On a Small Collection of Decapod Crustaceans from Fresh Waters in North Borneo" (*Tr. Zool. Soc. London*, 1900, pp. 93-95).

DOFLEIN, F.: "Amerikanische Dekapoden der k. bayerischen Staatssammlungen" (*SB. Akad. Muenchen*, Vol. 29, 1899, pp. 187-188).

— "Ueber eine neue Suesswasserkrabbe aus Columbien" (*Ibid.*, Vol. 30, 1900).

— "Ostasiatische Dekapoden" (*Abh. k. bayerischen Akad. Wiss.*, Vol. 21, 1902, pp. 626-628, 662-663).

HILGENDORF, F.: "Die Land- und Suesswasser-Dekapoden Ostafrikas" (in Moebius, K. *Deutsch Ostafrika*, Vol. 4, 1898).

LANCHESTER, W. F.: "On Some Malacostracous Crustacea from Malaysia in the Collection of the Sarawak Museum" (*Ann. Nat. Hist.*, Ser. 7, Vol. 6, 1900, pp. 255-257).

DE MAN, J. G.: "Note sur quelques Thelphusides recueillies par M. Pavie dans l'Indo-Chine" (*Bull. Soc. Philom. Paris*, Ser. 8, Vol. 10, 1898, pp. 36-52).

— "Description d'une espèce nouvelle du genre Potamon Sav. provenant du pays des Somalis" (*Ann. Mus. Genova*, Ser. 2, Vol. 19, 1898).

— "Zoological Results of the Dutch Scientific Expedition to Central Borneo. The Crustaceans. Part 2" (*Not. Leyden Mus.*, Vol. 21, 1899, pp. 67-132).

— "Description of a New Freshwater Crustacean from the Soudan" (*Pr. Zool. Soc. London*, 1901, pp. 94-104).

NOBILI, G.: "Viaggio del Dott. A. Borelli nella Republica Argentina e nel Paraguay. Crostacei Decapodi" (*Boll. Mus. Torino*, Vol. 11, No. 222, 1896).

— "Di una nuova varietà della Thelphusa dubia raccolta a Kazungula" (*Ibid.*, No. 262, 1896).

— "Viaggio del Dr. Enrico Festa nella Republica dell' Ecuador. Decapodi terrestri e d'acqua dolce" (*Ibid.*, Vol. 12, No. 275, 1897).

— "Decapodi e Stomatopodi raccolti dal Dr. Enrico Festa nel Darien, etc." (*Ibid.*, No. 280, 1897).

— "Supra alcuni Decapodi terrestri e d'acqua dolce" (*Ann. Mus. Genova*, Ser. 2, Vol. 19, 1898, pp. 9-14).

— "Intorno ad alcuni Crostacei Decapodi del Brasile" (*Boll. Mus. Torino*, Vol. 14, No. 355, 1899).

— "Contribuzioni alla conoscenza della fauna carcinologica della Papuasie,

- delle Molucche e dell' Australia" (*Ann. Mus. Genova*, Ser. 2, Vol. 20, 1899, pp. 261-264).
- NOBILI, G.: "Decapodi e Stomatopodi Indo-Malesi" (*Ibid.*, Ser. 3, Vol. 20, 1900, pp. 499-504).
- "Decapodi raccolti dal Dr. Filippo Silvestri nell' America meridionale" (*Boll. Mus. Torino*, Vol. 16, No. 402, 1901).
- "Viaggio del Dott. Enrico Festa nella Republica dell' Ecuador. Decapodi e Stomatopodi" (*Ibid.*, Vol. 16, No. 415, 1901).
- RATHBUN, M. J.: "Descriptions de nouvelles espèces de Crabes d'eau douce appartenant aux collections du Muséum d'histoire naturelle de Paris" (*Bull. Mus. Paris*, 1897, pp. 58-61).
- "Descriptions of Three New Species of Freshwater Crabs of the Genus *Potamon*" (*Pr. Biol. Soc. Washington*, Vol. 12, 1898, pp. 27-30).
- "The Decapod Crustaceans of West Africa" (*Pr. U. S. Mus.*, Vol. 22, 1900, pp. 282-285).
- "The Brachyura and Macrura of Porto Rico" (*Bull. U. S. Fish Comm. for 1900*, Vol. 2, 1901, p. 23).
- "Description des nouvelles espèces de *Parathelphusa* appartenant au Muséum de Paris" (*Bull. Mus. Paris*, 1902, p. 184 ff.).
- WEBER, M.: "Die Decapoden Crustaceen des Suesswassers von Sued-Afrika" (*Zool. Jahrb. Syst.*, Vol. 10, 1897, p. 156).

According to Ortmann (1897) the family of *Potamonidae* Ortm. (= *Thelphusidae* Dan.) is divided into four subfamilies: *Potamonina* Ortm., *Deckeniina* Ortm., *Potamocarcinina* Ortm.,<sup>1</sup> and *Trichodactylina* Ortm. The first two belong to the Old World, the last two inhabit the New World.<sup>2</sup>

#### 1. Subfamily: POTAMONINÆ.

The subfamily *Potamonina* is in very poor condition, systematically. Not only our knowledge of the very numerous species is rather incomplete, but also their arrangement into genera and subgenera is by no means satisfactory. Generally, it seems that we can distinguish two genera: *Parathelphusa* M.-E. and *Potamon* Sav. (= *Thelphusa* Latr.), to which possibly a third one is to be added,

<sup>1</sup> — *Pseudothelphusina* Ortmann and Rathbun (1898, p. 508). The division into genera varies considerably with Ortmann and Rathbun respectively (see below), and the name of the subfamily depends on the classification accepted.

<sup>2</sup> According to Alcock (*Journ. Asiat. Soc. Bengal*, Vol. 69, 1900, p. 279), also *Gecarcinucus* (one species in the peninsula of India), which was placed hitherto with the family *Gecarcinidae*, belongs to the *Thelphusidae* (= *Potamonidae*). If this is so, we ought to create, possibly, a separate subfamily for this genus.

the very incompletely known *Erimetopus* of Rathbun. The value of a few other genera, created by various authors, is extremely doubtful.

*Parathelphusa* is represented by typical species in the northern parts of India, in Burma, Siam, Anam, Malacca, Southern China (Hongkong and Canton), and in the Sunda Islands: Sumatra, Borneo, Java, extending to Timor and New Guinea. With the same genus some other forms have been classified which are found in certain parts of Africa (Congo basin and Nile river); but these have been placed by the present writer in a subgenus (*Acanthothelphusa*) of *Potamon*, since they differ in their general shape very strikingly from the Asiatic species of *Parathelphusa*. Unfortunately these African species are very poorly known; only of the Nile species figures have been published (Milne-Edwards and Hilgendorf), and according to these it is impossible to unite this species and its supposed allies with *Parathelphusa*.<sup>1</sup>

As regards the genus *Potamon*, it is divided into several subgenera, which, however, are not very sharply defined. Aside from the doubtful subgenus *Acanthothelphusa* just mentioned, there are three of them which are generally recognized: *Potamon* (sens. strict.), *Potamonautes* Macl., and *Geothelphusa* Stps.<sup>2</sup>

The centre of the subgenus *Potamon* is, no doubt, in India and Farther India. Thence it extends eastward to the greater Sunda Islands (Sumatra and Java); it is found in the Philippine Islands, but does not advance any farther in this direction. Northward it enters China, where it is known from the Yang-tse-Kiang (see Doflein, 1902, p. 662). It does not seem to pass beyond the Himalaya Mountains to the north, but extends considerably westward (possibly in a single species), going through Persia to the Transcaspian countries, crossing the Caucasus Mountains and extending to the Crimea; from Mesopotamia it extends to Syria and Asia Minor, where it reaches the Mediterranean countries, and here it is found in Northern Egypt, Turkey, Greece, Italy, Sicily, and

<sup>1</sup> Possibly *Platythelphusa* A. M.-E. (see Hilgendorf, 1898, p. 21) from Lake Tanganyika also belongs here.

<sup>2</sup> I disregard, for the present, the subgenus *Perithelphusa* de Man (1899, p. 70), which contains apparently rather primitive forms of *Geothelphusa*, and, on account of its exclusive occurrence in Borneo, may be left united with *Geothelphusa*. As to *Platythelphusa*, see the last note. As to *Hydrothelphusa* A. M.-E., see below.

farther in Algiers as far as Oran.<sup>1</sup> It is a remarkable fact that this subgenus is entirely absent from Africa proper, *i.e.*, the part of it that lies to the south of the Sahara Desert.

The subgenus *Potamonautes*, on the contrary, has its chief centre of distribution in tropical Africa. It has been found, beginning at Liberia, all along the western coast as far as Mossamedes. It is found in the interior, in the region of the upper Zambesi (Kazungula), extends over Transvaal to the Cape Colony, and northward all along the eastern coast (Natal, Mozambique) to German East Africa. Also in the eastern part of the interior it is represented, for instance, in the headwaters of the Nile (Victoria Nyanza) and in the Somali country. From the upper Nile it extends down the Nile valley as far as Bahr-el-Gebel in the Egyptian Soudan. It is also found on the Island of Socotra and in Madagascar, although the species of the latter island do not seem to belong to the typical form of this subgenus.<sup>2</sup>

<sup>1</sup> A. Milne-Edwards reports a species that is identical with an Indian (*P. leschenaudi* (M.-E.)) from Mauritius: this locality, however, lacks confirmation. As regards the Madagassian species of *Potamon*, their systematic position is doubtful, and they possibly do not belong to this subgenus. Compare next note.

<sup>2</sup> Three species of *Potamon* are known from Madagascar. *P. goudoti* (M.-E.) (see A. Milne-Edwards, 1869, p. 172, Pl. 8, Fig. 4) is a peculiar form, but its postfrontal crest distinctly points to *Potamonautes*. A. Milne-Edwards compares it with *P. obesum* A. M.-E. from Zanzibar, and indeed it seems to be closely related to it. The latter species is also an abnormal type of *Potamonautes*, and forms with several others a group that is peculiar to East Africa; but there is no reason to separate this group from *Potamonautes*, and thus we may safely regard *P. goudoti* as a *Potamonautes*. The second species is *P. madagascariense* (A. M.-E.) (*Ann. Sci. Nat. Zool.*, Ser. 5, Vol. 15, 1872). As to this form, the diagnosis of which is very brief, and which has not been figured, its author says that it is a true *Thelphusa* (*i.e.*, subgenus *Potamon*), but this seems hardly correct according to the description of the postfrontal crest, which is said to be simply interrupted in the middle, while the median parts of it are not advanced beyond the rest. This would better agree with *Potamonautes*. The third species is regarded by A. Milne-Edwards (*Ibid.*, 1872) as the type of a separate genus, *Hydrothelphusa* (*H. agilis* A. M.-E.). This genus is said to be characterized by the flat carapace, which is scarcely dilated and almost quadrangular, and by the horizontal front. The postfrontal crest is distinct and interrupted. Since no figure is given, it is hard to form an opinion as to the relation of this form to others, but it seems to be very peculiar.

Thus it seems that the Madagassian species of *Potamon* show, in some respects, a distinct relation to East Africa and the subgenus *Potamonautes*, while in others they appear quite peculiar. (This is opposed to the opinion expressed by myself in 1901, p. 1290, footnote.)

The main range of *Potamonautes* in Africa seems to be almost continuous, but absolutely isolated from it is a secondary centre in South Asia. Here this subgenus is represented in India, and thence it extends to Farther India, and reappears on some of the islands: Pulo Condore on the coast of Cochin China, in the Philippine Islands, Celebes and New Guinea. These latter localities are distinctly discontinuous.

The third subgenus, *Geothelphusa*, undoubtedly has its centre in the extreme East, and it is most characteristic for the Malaysian Islands. On the Asiatic continent it seems to be absent; but it is found abundantly in Sumatra, Java, Borneo, and extends eastward over Aru Island and New Guinea to North Australia, where it is found on the Cape York Peninsula, and in Queensland as far as Port Mackay.<sup>1</sup> Northward this subgenus ranges over the Philippine and Loo-Choo Islands to Japan, where it reaches its northernmost station in the neighborhood of Tokyo.

On the continent of Asia typical species of this subgenus have not been found; indeed a few small species from India have been described which might be united with this subgenus, but this is by no means sure.

But this identical subgenus, *Geothelphusa*, is apparently found in another locality isolated from the rest of the range: this is *P. berardi* (Aud.) from Egypt (Nile river). This species, however, is also morphologically isolated from the rest; and further, this subgenus is recorded by Rathbun from Liberia (*P. macropus* Rthb., 1898), and some species from East and Central Africa, related to *P. obesum*, mentioned above, resemble, in the reduction of the postfrontal crest, the subgenus *Geothelphusa*,<sup>2</sup> while on the other hand they are undoubtedly related to the subgenus *Potamonautes*. It is quite possible also that *P. berardi* from Egypt (Kairo southward to Mount Elgon) belongs to this East African group. In my opinion, all these species do not properly belong to *Geothelphusa*, and we have to deal here again with a case of convergency: the

<sup>1</sup> According to de Man, an Australian species (*P. transversum* (Mrtz.)) is also found in the Fiji Islands; but this lacks confirmation.

<sup>2</sup> These are *P. obesum* (A. M.-E.), Zanzibar; *P. emini* Hlgdf., *P. newmanni* Hlgdf., *P. pilosum* Hlgdl. (Hilgendorf, 1898), all three from East Africa and the region of the Great Lakes. Possibly *P. socotrense* Hilgendorf (1883, *Zeitschr. d. Naturw.*, Ser. 4, Vol. 2) — *P. granosum* Koelbel (*SB. Akad. Wien*, Vol. 90, 1885) belongs here.

tendency to reduce the postfrontal crest has developed in the East African forms independently from the typical *Geothelphusa*, and the East African (possibly also the Liberian) species form a peculiar branch of *Potamonantes*.

The genus *Erimetopus* of Rathbun is found so far only in the Congo basin.

Considering the distribution of the subfamily *Potamonina* in general, we see that it is continuous over the whole of tropical Africa, then it extends through the Nile valley into the Mediterranean regions and connects with the Asiatic range, which goes from Syria over Mesopotamia, Persia to India, China and the Malaysian archipelago, over which it finally reaches Northern Australia and Japan. This whole range is practically continuous, only the larger continental islands (disregarding the smaller ones), Madagascar and the Sunda Islands, the Philippines, New Guinea and Japan, constituting breaks in the continuity.

Within this large area, however, we are able to distinguish two main divisions: an African, characterized by the prevalence of the subgenus *Potamonantes*, the complete lack of the subgenus *Potamon* (and possibly of *Geothelphusa*), and an Asiatic-Australian division, characterized by the prevalence of the subgenus *Potamon*, the presence of *Geothelphusa* (in its eastern part), and the scarcity of *Potamonantes*. Both divisions are practically connected by the Nile valley; this connection, however, does not seem to represent the original condition, but suggests a secondary one, since different types are here associated which are not at all related to each other. Species of *Potamonantes*, to which subgenus, according to our opinion, *P. berardi* also belongs, migrating northward from the Soudan, have met here in Lower Egypt a species of the subgenus *Potamon* (*P. fluviatile*), which had migrated westward from India. Both subgenera entered the Nile valley from different directions and accidentally became occupants of the same territory, but the Nile valley is not the route of migration by which African species migrated into Asia or *vice versa*.

Aside from this narrow connection, the fauna of freshwater crabs of tropical Africa is very sharply characterized and isolated from Asia,<sup>1</sup> and the fact is worth special mention that North Africa

<sup>1</sup> The peculiarity of the African fauna is emphasized by the doubtful forms of *Parathelphusa* (or *Acanthothelphusa*), and by *Erimetopus*.



(Lower Egypt and Algiers) points, like the whole of the Mediterranean region, to India, from which locality the species present there, *P. fluviatile* (Latr.), has apparently migrated in an east-westerly direction over Persia, Mesopotamia and Syria. *P. fluviatile* has been actually recorded from western India; at any rate the most closely allied species to this one are found in India and China.

Other remarkable facts in the distribution of this subfamily may be summed up thus:

1. The Asiatic as well as the African part of the range is occupied by the subgenus *Potamonautes*. It is impossible to say which was the original home of *Potamonautes*, but this much is evident, that it must have been present in both parts at a comparatively early time, it being probably older than *Potamon* sens. strict. In Africa *Potamonautes* attained its highest development, being the prevailing type there and showing great variety.

2. Madagascar, while belonging distinctly to Africa in its fauna, possesses some rather peculiar types.

3. The subgenus *Potamon* originated in Asia, apparently at a time when there was no connection any more with tropical Africa or Madagascar. The immigration of *Potamon* into the Mediterranean countries, across Persia, etc., is probably a comparatively recent one, since the route of immigration is easily traced and occupied by one single species.

4. The Malaysian and Philippine Islands, Japan and North Australia possess in *Geothelphusa* a very peculiar group. This distribution of *Geothelphusa* does not correspond to that of *Parathelphusa*, *Potamonautes* and *Potamon* sens. strict., which are also found in the Malaysian Islands. *Potamonautes* and *Parathelphusa* are similar in this respect, possessing on the Sunda Islands only scattered stations (as far as New Guinea), which by their discontinuity express an ancient condition. *Potamon* points directly to an Indian origin, extending only to Sumatra, Java and the Philippines, but going not any farther to the east.

5. The position of *Parathelphusa* is hard to understand. If it is really absent in Africa, as we believe, its distribution in Asia is rather eastern than western, being chiefly found in Farther India. Its extension over the Sunda Islands to New Guinea points to old conditions. Since the morphological relations of *Parathelphusa* to the rest of the subfamily are not well understood, it is better to exclude it from our further consideration.

Supposing that this subfamily must have had once a more or less continuous distribution, we are to draw from this the following conclusions as to the geographic conditions of the past:

1. *Africa and India must have been connected once. This connection, however, was not by way of North Africa, Arabia and Persia, and is possibly identical with that from Africa over Madagascar to India, discussed above (see No. 5, p. 295).*
2. *Madagascar must once have been a part of Africa.*
3. *The Indo-Malaysian Islands, including the Philippine Islands, Loo-Choo Islands and Japan, must have been once connected not only between themselves, but also with New Guinea and North Australia (as indicated by *Geothelphusa*). On the other hand, the distribution of the typical forms of *Potamon* indicates that some of these islands (Sumatra, Java, Philippines) were once connected with the continent of Asia. Then, again, by *Potamonäutes* (and *Paräthelphusa*) the former continuity of the whole region from India to New Guinea is indicated (see p. 295). It is evident that here repeated and important changes of the mutual connections have taken place at different periods of the past.*

The history of the subfamily of *Potamoninae* would then be this: Its centre lies in an Afro-Indian continental mass, which was divided subsequently into two parts, tropical Africa and India. From India the subfamily extended at a very early period over the Sunda Islands, Philippine Islands, which consequently must have formed a part of the continent, and this continental connection extended as far as New Guinea and Australia, but not without repeated interruptions and changes. In the region of unstability and change lies the home of the subgenus *Geothelphusa*, which was able at a certain time to go as far north as Japan. A separate branch of the subgenus *Potamon* was sent out from India westward, which finally reached the Mediterranean countries, where it met in the lower Nile valley a branch of the African subgenus *Potamonäutes* which came down the Nile from the south.

## 2. Subfamily: *Deckeniinae*.

The second subfamily of the Old World, the *Deckeniinae*, contains only one genus, *Deckenia* Hlgdf. (see Ortmann, 1897, p. 314), of which three species have been described:

*D. imitatrix* Hlgdf. Interior of British East Africa: Taro (Hil-

gendorf, 1898, p. 23) and Somali country (de Man, 1898, p. 270).

*D. mitis* Hlgdf. (1898, p. 24). German East Africa and British East Africa (Mombas).

*D. alluaudi* A. M.-E. and Bouv. (= *cristata* Rthb.). Seychelle Islands.

The *Deckeninae* are, as is expressed by their morphological characters (Ortmann, 1897, p. 297), a highly specialized group of the family which may be connected without hesitation with the genus *Potamon*, and possibly with the African branch of it. This subfamily is a group localized in East Africa, and the presence of one of the species in the Seychelles indicates a former connection of these islands with East Africa. It is quite probable that this connection is an additional proof for that old Afro-Indian landbridge discussed above, which included Madagascar (see No. 5, p. 295, and No. 1, p. 305).

### 3. Subfamily: *Potamocarcininae*.

The subfamily *Potamocarcininae* (= *Pseudothelphusinae*) is restricted to America and is wanting in the Old World. The systematic arrangement of it is a matter of discussion, since the two revisions published by Rathbun and Ortmann do not agree as to the principles of division.

Regarding the subfamily as a whole, its range comprises the following parts: West Indies—Greater Antilles: Cuba (including the Isle of Pines), Hayti, Porto Rico (including Santa Cruz); Lesser Antilles: Guadeloupe, Dominica, Martinique, Sta. Lucia. On the continent its range begins in Mexico; the northern boundary is marked by a line beginning in Tepic Territory, running through the States Jalisco and Guanajuato to Vera Cruz. Thence the range covers the southern parts of Mexico, Guatemala, Nicaragua, Costa Rica and Colombia, and extends eastward over Venezuela (including Trinidad) and Guyana. In a southerly direction it passes from Colombia into Ecuador, Peru and to Northern Bolivia. In the latter region it is found in the Cordilleras and the tributaries of the upper Amazonas river. An isolated locality is Pará, on the southern side of the mouth of the Amazonas river (*Pseudothelphusa agassizi* Rthb.).

In order to get an idea of the distribution of the different genera

of this subfamily, it is necessary to discuss the systematics of it. Ortmann distinguishes four genera: *Potamocarcinus*, *Epilobocera*, *Hypolobocera* and *Kingsleya*, while Rathbun accepts the following: *Epilobocera*, *Potamocarcinus*, *Pseudothelphusa* and *Rathbunia*. Generally, Ortmann's *Potamocarcinus* corresponds to the genera *Potamocarcinus* and *Pseudothelphusa* of Rathbun, and the close affinity of these two is also admitted by Rathbun, so that their union (under *Potamocarcinus*) is well supported. But in this case, we are to exclude from *Potamocarcinus* the species *sinuatifrons* Kgs. (and Ortm., nec A. M.-E.) = *haytensis* Rthb., which belongs to *Epilobocera*. If we add this latter species to Ortmann's *Epilobocera*, this genus corresponds exactly to *Epilobocera* Rathbun. *Hypolobocera* of Ortmann is classed by Rathbun with *Pseudothelphusa* (*Potamocarcinus* of Ortmann), and rightly so, as we now believe. *Kingsleya* Ortmann is put by Rathbun with *Potamocarcinus* (sens. strict.); this, however, does not seem to be justified, since then the very peculiar shape of the orbita is neglected. While in all other forms of the subfamily the lower orbital margin possesses on the inner end a suborbital lobe, which may unite with the front, in *Kingsleya* the lower orbital margin itself joins the front, while the suborbital lobe is hidden. This character, connected with the extremely reduced condition of the exopodite of the third maxilliped, which also does not find its like in the whole subfamily, fully warrant, in our opinion, the creation of a separate genus. The genus *Rathbunia* of Nobili is founded upon a single species, and its chief character is taken from the shape of the meropodite of the third maxilliped, which is narrower than usual at the proximal end. In all other respects this genus agrees absolutely with *Pseudothelphusa* (resp. *Potamocarcinus* of Ortmann), and a generic separation does not seem to be necessary.

As a compromise between both generic divisions I should like to suggest the following:

Genus: *Epilobocera* Stps. (corresponding fully to *Epilobocera* Rathbun).

Genus: *Potamocarcinus* M.-E. (= *Potamocarcinus* Ortm. (excluding *sinuatifrons* Ortm. = *haytensis* Rthb.) + *Hypolobocera* Ortm.).

1. Subgen. *Potamocarcinus* M.-E. (genus, according to Rathbun, excluding the species *latifrons* Rand.).

2. Subgen. *Pseudothelphusa* Sauss. (= genus *Pseudothelphusa* Rathb.).

3. Subgen. *Rathbunia* Nobili (= genus Nobili and Rathb.).  
Genus *Kingsleya* Ortm.

It is entirely a matter of taste whether one prefers to regard *Potamocarcinus*, *Pseudothelphusa* and *Rathbunia* as genera or subgenera. This much, however, is evident, that they are much more closely allied to each other morphologically than to either *Epilobocera* or *Kingsleya*. Judging from the third maxillipeds (which furnish a good criterion in this respect), *Epilobocera* should be regarded as the most primitive form, *Potamocarcinus* (in the largest sense) would be typical and *Kingsleya* the most specialized.

This division into three genera corresponds well to the geographical distribution of the different forms (see Rathbun, 1898, pp. 532-537).

*Epilobocera* contains six species which are restricted to the Greater Antilles: Cuba, Isle of Pines, Hayti, Porto Rico and Santa Cruz Island.

*Potamocarcinus* (in the widest sense) contains 47 species<sup>1</sup>, which cover the whole continental range of the subfamily from Mexico to Bolivia and Pará, the Lesser Antilles and of the Greater Antilles, Cuba and Hayti. The subgenus *Pseudothelphusa* has the same range, while of the two species of *Potamocarcinus* (sens. strict.) one is found in Guyana, the other in Costa Rica. *Rathbunia* is known only from Darien. *Kingsleya* is so far known only from Guyana.

The range of the subfamily on the continent seems to be perfectly continuous; only *P. agassizi* from near Pará appears to be more or less isolated. The most closely allied forms to this one (*reflexifrons* Ortm. and *denticulatus* M.-E.) are found in the region of the upper Amazonas and in Guyana respectively, so that this locality (Pará) is possibly connected with Guyana. There is, however, the other possibility, that along the course of the Amazonas river a connection exists between its lower part (Pará) and its upper (upper Amazonas). A very important fact is that Pará is

<sup>1</sup> Forty-two species mentioned by Rathbun, one described subsequently by Doflein (1900, *P. principessa*, Colombia), one described by Nobili (1901, *P. caputii*, Ecuador); these forty-four belong to *Pseudothelphusa*. Two species belong to *Potamocarcinus* and one to *Rathbunia*.

the only locality known for this subfamily to the south of the Amazonas river, at least in Brazil. Generally, we may call this river the southern boundary of the range of the subfamily, although in the Cordilleras of Peru and Bolivia *Potamocarcininae* are found more to the south.

The localities of this subfamily in the West Indian islands are now separated from the main range on the continent. Here we can distinguish two groups: the Greater Antilles possess as a characteristic type the genus *Epilobocera*, which is found nowhere else. At the same time we have in Cuba three species of *Pseudothelphusa*, of which one (*americana*) is also found in Hayti. This same species, *P. americana* Sauss., is found largely distributed in Mexico (States of Guanajuato, Morelos, Puebla, Guerrero, Oaxaca), and, further, another Cuban species (*terrestris* Rthb.) has also been reported from Mexico (Jalisco and Tepic), while the third species (*affinis* Rthb.) is restricted to Cuba.<sup>1</sup>

The second group within the West Indies is formed by the islands of Gaudeloupe, Dominica, Martinique, St. Lucia, where one species (*P. dentata* (M.-E.)) is found. According to Rathbun (1898, p. 524), the most closely allied forms to this are *P. garmani* Rthb. from Trinidad and Venezuela, and *P. fossor* Rthb. from Venezuela.

The above chorological and systematic facts justify the following conclusions:

1. *The distribution of the Potamocarcininae in Central and South America is remarkable, in so far as it does not go southward beyond the Amazonas river.*
2. *The West Indian islands must have been once connected with Central and South America. The freshwater crabs of the Greater Antilles point to a connection with Mexico, as well as to a connection between themselves, after they were separated from the mainland (Epilobocera). The freshwater crabs of the Lesser Antilles point to a connection with Trinidad and Venezuela.*

#### *Connection of the Potamocarcininae and Potamoninae.*

As is accepted by all authors, the affinity of the *Potamocarcininae* of the New World with the *Potamoninae* of the Old World is beyond question, and this affinity is expressed by their position as

? <sup>1</sup> This locality, given for a specimen from the old collection of Guérin in Philadelphia, needs confirmation.

two subfamilies within the same family, *Potamonidae*, which has never been disputed.<sup>1</sup> Consequently the idea suggests itself that both subfamilies have a common origin, or have descended the one from the other. Transitional forms between them are not known; this, however, is not astonishing if we consider their geographic isolation.

The present writer has called attention to the presence in Central Africa of a group of *Potamon*, which he has designated as the subgenus *Acanthothelphusa*. These species have been united by others with *Parathelphusa*, which classification we do not consider to be correct. Although these species are very poorly known, it seems impossible to unite the type-species of *Acanthothelphusa* (from the Nile) with *Parathelphusa*, and it would be well to examine the other species more closely with a view to their possible relation to the American *Potamocarcininae*.

Whether this prove to be so or not, this much is unquestionable, that the West African *Potamoninae* are geographically most closely approached by the South American *Potamocarcininae*, and thus a former connection of the respective parts, West Africa and northern South America, is suggested (see Ortmann, 1901, p. 1291).

#### 4. Subfamily: *Trichodactylinae*. (See Fig. 4.)

Finally, we are to consider the subfamily *Trichodactylinae* Ortm., which is divided, according to Ortmann (1897, p. 298), into two genera, *Trichodactylus* Latr. and *Orthostoma* Rand., which latter generic name, however, is to be abandoned as preoccupied. Its place is to be taken by *Sylviocarcinus* or *Dilocarcinus* M.-E., 1853. But even *Trichodactylus* and *Dilocarcinus* (in its largest sense including *Sylviocarcinus*, according to Ortmann, and being identical with *Orthostoma*) are not always sharply defined, and, further, the

<sup>1</sup> According to Ortmann (*Zool. Jahrb. Syst.*, Vol. vii, 1893, p. 430), the *Thelphusidae* (*Potamonidae*) are possibly derived from *Menippidae*—i.e., primitive *Xanthidae* (in Alcock's sense). They are primitive *Cyclometopa*, which, however, in certain characteristics, probably connected with their habits, are more highly and abnormally developed, and exhibit (due to convergency?) similarities to the *Cutometopa*.

Alcock (*Jour. Asiat. Soc. Bengal*, V. lviii, Part 2, No. 1, 1899, p. 3) is inclined to regard the *Thelphusidae* as descendants of the *Osiina* or *Eriphiina* (higher *Xanthidae*), and takes them for very highly specialized *Cyclometopa*.

Both views agree in that the family *Xanthiidae* is supposed to be the ancestral stock of these freshwater crabs.

distinction of species seems to be very arbitrary within these genera. Up to the present, about five or six species of *Trichodactylus* and about fourteen species of *Dilocarcinus* have been described. In the following we shall discuss them all together.

The subfamily covers an area that comprises the larger southern half of Brazil (Bahia, Rio de Janeiro, Goyaz, Minas Geraes, S. Paulo, Sta. Catharina, Rio Grande do Sul). It is found in Paraguay, and in the Argentinian provinces: Misiones, Chaco and near La Plata (Ensenada).<sup>1</sup> Further, species of *Trichodactylinae* are very abundant in the Cordilleras, in the region of the headwaters of the Amazonas river, namely, in Bolivia (pro-



FIG. 4. Distribution of the Crabs of the subfamily *Trichodactylina*.

? long to the upper Madeira), in Peru (rivers Ucayali, Huallaga), and in the Marañon at Nauta and Loreto (Ecuador). Since there are also representatives known from the lower Amazonas (Island Marajo), all these localities named seem to form a continuous area, which extends from the Amazonas river southward to La Plata, and from the Atlantic Ocean westward over Brazil, Paraguay and Argentina to Bolivia and Peru, where it reaches the eastern slopes of the Cordilleras. Apparently isolated ? from this area, several species are found in Guyana, and, finally, one species (*Trichodactylus quinquedentatus* Rthb.) is known from the upper parts of the river Magdalena in Colombia, and from the Escondido river in Nicaragua.

It is quite possible that the isolated stations in Guyana, Colombia and Nicaragua will be connected by subsequent discoveries (Colombia is very near to the localities of the upper Amazonas), and then we would have for this subfamily a continuous range, which comprises the whole of South America southward to La Plata, and from the Atlantic Ocean to the eastern slopes of the Cordilleras, and which extends in Central America as far as

<sup>1</sup> I have received from the La Plata Museum specimens of *Dilocarcinus panoplus* (Mrt.) from Ensenada.



Nicaragua. It is to be remarked that none of the localities is situated in the drainage of the Pacific Ocean, but all are in that of the Atlantic.<sup>1</sup>

This distribution does not offer any remarkable facts. The *Trichodactylinae* seem to belong to the tropical parts of the Atlantic slope of South America, and their centre is somewhere in Brazil; from Brazil they extend in every direction until, in the east the Atlantic Ocean, in the west the Cordilleras, in the south the climate of Argentina form barriers. To the north the most advanced station is in Nicaragua; here no natural boundary (climatic or topographic) is marked.

Further speculations as to the distribution of this subfamily do not seem to be very promising until we are better acquainted with the chorological facts. The whole appearance presented by the distribution is a recent one, probably it is continuous and, in most directions, limited by natural boundaries. In this respect it is strikingly distinguished from the other groups of the family *Potamonidae* discussed above.

I have the impression that the *Trichodactylinae* are not so closely connected, systematically, with the other subfamilies of the *Potamonidae* as was believed hitherto. In fact, transitional forms to any of the other subfamilies are not known, and the *Trichodactylinae* are morphologically isolated and sharply defined. Moreover, the whole "habitus" of these crabs is so entirely different from that of the *Potamocarcininae* that it is worth while to revise the systematic relations of these groups. As I venture to imagine, it will be found, possibly, that the *Trichodactylinae* form a group that is much more sharply isolated, systematically, and that has little to do with the family *Potamonidae*. This much is evident: according to its morphologic isolation, we ought to expect that the *Trichodactylinae* are a comparatively ancient group; but this is contradicted by their distribution, which possesses a remarkably recent character.

These are the reasons why we shall exclude the *Trichodactylinae* from our further discussions.

<sup>1</sup> This is contrary to what we have in the *Potamocarcininae*, which are found also on the Pacific slope in Ecuador, and especially in Central America and Mexico.

## PART II. RECONSTRUCTION OF ANCIENT GEOGRAPHIC CONDITIONS.

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OSBORN, H. F. "The Geological and Faunal Relations of Europe and America during the Tertiary Period and the Theory of the Successive Invasions of an African Fauna" (*Science*, April 18, 1900, pp. 561-574; see also *Ann. N. Y. Acad. Sci.*, Vol. xiii, 1900, pp. 1-72).

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<sup>1</sup> Only the more important papers are given in the following list. Others, quoted only incidentally, shall find their place in footnotes.

<sup>2</sup> I quote only the following two papers of von Ihering, although he has published several more on these and kindred subjects. But these two contain the essence of his theories.

North American Geographic Development" (*Amer. Journ. Sci.*, Vol. xlv, 1893).

HILL, R. T. "The Geological History of the Isthmus of Panama and Portions of Costa Rica" (*Bull. Mus. Harvard*, Vol. xxviii, 1898).

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In the following we shall endeavor to answer the questions: *What connections are suggested by the distribution of the freshwater Decapods, and Is there any other evidence, in the first place, of a geological character to support them?* The solution of these questions will furnish us the key for the reconstruction of the old geographic conditions.

If we recall the connections suggested by the distribution of the freshwater Crustaceans, we can collect them in the following list:

1. *Connection of northeast Asia with northwest America across Bering Sea* (see pp. 290, 291, 295).

2. *Connection of east Asia with Australia* (see pp. 295, 305).

3. *Connection of south Asia with Madagascar and Africa* (see pp. 295, 305, 306).

4. *Connection of New Zealand with Australia* (see p. 295).

5. *Connection of Australia (resp. New Zealand) with South America* (see p. 295).

6. *Connection of the West Indies with Central, resp. South America* (see pp. 295, 309).

7. *Connection of South America with Africa* (see p. 310).

Other important questions arose out of the distributional facts, which may be classified under the following heads:

8. *General relations of North, Central and South America* (see pp. 295, 309).

9. *Relations of Africa to the rest of the world* (see pp. 303, 304).

10. *Relations of Europe to Asia (and Africa)* (see pp. 291, 295, 304).

We shall take up these different items in the order here indi-

cated. But before we do so, we have to say a few words by way of explanation and introduction, characterizing the value of the study of the freshwater Decapods for these purposes.

In all the following discussions, the fundamental supposition has been made that freshwater crayfishes, as well as freshwater crabs, do not possess any exceptional means of dispersal; that is to say, that they are restricted to fresh water and cannot exist in salt water; that they cannot leave the water for any continued period, and consequently cannot migrate over land to any extent; and, finally, that they do not possess in any stage of their life, and especially not in the egg or larval stage, any means or devices which permit their passive transport. We may specify these three points in the following way:

1. The restriction to fresh water is not absolute. There are a few exceptions, namely:

*Potamobius pachypus* (Rthk.) is found in the Black and Caspian Seas in brackish and salt water.

*Potamobius trowbridgei* (Stps.) has once been collected in salt water at Monterey, California (Faxon, 1898, p. 666).

*Cambarus uhleri* Fax. is characteristic for the marshes of the coast of Maryland, and lives in fresh, brackish, and salt water.

*Cambarus montezumæ* Sauss. has been found, in one case, in a salt lake in Mexico (Lake Tezcoco, near City of Mexico; see Faxon, 1885, p. 123).

*Potamon fluviatile* var. *ibericum* (Bisb.) is found in fresh water and salt water of the Caspian Sea (see Ortmann, 1897, p. 302).

On account of the small number of these cases, we have to regard them as exceptional, and they are, no doubt, secondary adaptations. In fact, none of these species is a true saltwater form, they being always more or less euryhalin, and frequenting also brackish or freshwater. Thus we may say, generally, *that both, crayfishes and crabs, discussed here, are true freshwater animals, and preëminently so, and that a migration across oceans or parts of oceans is practically excluded.*

2. Being animals breathing by gills, crayfishes and freshwater crabs cannot leave the water. This rule is without exception with the *Potamobiidæ* and *Parastacidæ*; they may leave the water for a short time, but a prolonged stay outside of it is always fatal. There are only a few species in North and South America, and in Aus-

tralia, burrowing in mud, which leave the water habitually; but they always have to return to the water to moisten their gills, and their burrows end in water. The forms most adapted to a subterranean life are probably the two species of *Engaeus* in Tasmania. In general, for the crayfishes, tracts of land without water (deserts) are absolute barriers.

The *Potamobiidae* lead a rather amphibic life and leave the water, in many cases, habitually. Yet they always depend on the presence of water and cannot go far out of easy reach of it. Some of the species (*Potamon fluviatile* in Persia, etc.) live in steppes, where there is a scarcity of water, but here they always are found near some kind of water supply. In general, they also cannot exist in deserts.

3. As in all other Decapods, also in crayfishes and freshwater crabs the eggs are carried and hatched under the abdomen of the female. There is, as far as we know, no free metamorphosis of the young (known in *Potamobius*, *Cambarus*, *Potamon*), and the young hatch in a stage similar to the parents. Thus there seems to be no means which effect, under normal conditions, an increased facility of dispersal in an active or passive way among the young ones. There may be, occasionally, a passive transport by other animals (water fowl), but such cases can only be exceptions and have never been observed. The whole character of the distribution of the different species is against the assumption of exceptional means of dispersal.

#### 1. CONNECTION OF NORTHEAST ASIA WITH NORTHWEST AMERICA BY WAY OF BERING SEA.

A connection of northeast Asia with northwest America is postulated, as we have seen above, by the presence of *Potamobiidae* in the region of the Amur river, Korea, and north Japan on the one side, and in western North America on the other; the direction of this connection is indicated by the presence of *Potamobius nigrescens* (Stps.) in Unalaska.

This connection is mentioned by Jacobi (1900) under his "regions of dispersal" ("Ausbreitungsgebiete"), and is called by the name of "Berings-Strassen-Ausbreitungsgebiet." This is well known among zoogeographers. In fact, for an explanation of the very peculiar conditions of distribution of many animals of the northern hemisphere, a former connection of the northern land

masses of the Old and New Worlds is absolutely necessary, and the similarity of the land faunas of both parts, which is not explained by the present conditions, is so strong that these regions (northern Eurasia and North America) have been united by certain authors into *one* zoogeographical region, the Holarctic. As to the location of this connection, two ways are possible: either from Siberia to Alaska, or from Labrador over Greenland to Scandinavia. The latter connection, which has been discussed, from a geological standpoint, chiefly by Suess and Neumayr (for older times, Mesozoic and Tertiary), and, from a zoogeographical view by Scharff (for the Pleistocene), may be disregarded for our present purpose; there is no indication for its existence among the crayfishes. But the latter support strongly, as has been said, the other connection over Bering Strait.

Viewed from the tectonic side, this connection is quite possible. The old rocks of northeast Asia are continued into northeastern Siberia (east of the rivers Lena and Aldan) to the river Kolyma,<sup>1</sup> and farther, toward the Arctic Ocean and Bering Sea, and similar rocks are found in Alaska; and further, the chain of the Aleutian Islands is, according to Suess, another proof for the tectonic unity of the lands east and west of Bering Sea.

As regards the time of existence of this land bridge, we have to assume it during almost the whole of the Tertiary period. Osborn (1900) takes its existence for granted and demonstrates (p. 568) that during Eocene, Miocene and upward to the Pliocene, a regular exchange of the faunas of Eurasia and North America took place. In the older Pleistocene (p. 571) this connection still existed, but was interrupted in the middle Pleistocene (p. 572).

If we put the question, whether and how far this land bridge goes back in Pretertiary times, we have to consult first Neumayr's opinion as to the distribution of the Jurassic oceans and continents (1890, map, p. 336). It is true, in Siberia, deposits of Lower Jurassic age are not known, and possibly Siberia was land during this time<sup>2</sup>. There are found here, however, deposits belonging to

<sup>1</sup> See Tscherski, *Sap. Akad. St. Petersburg.*, Vol. 73, Append. 5, 1893 (Russian); Review in *N. Jahrb. Mineral.*, etc., 1896, Vol. 2, p. 318.

<sup>2</sup> Land and freshwater deposits of Jurassic age are largely distributed in Siberia as coal-bearing strata. Compare the geological investigations connected with the great Siberian railroad, by Obrutchev, Gerassimow, Gedroiz, Jaworowsky. Reviews in *N. Jahrb. Mineral.*, 1899, Vol. 2, p. 111-116.

the Upper Jurassic (Neumayr, 1890, p. 329), which reach the Pacific Ocean. Beds of the same age are known on the Aleutian Islands and in Alaska. These deposits exhibit a peculiar character, which has been called the boreal or arctic type, and in this respect the Jurassic beds of the western coast of North America are very important, since they agree with the boreal type. Neumayr concluded from this that the Upper Jurassic Polar Sea sent an extension southward along the western coast of North America into the North Pacific, and its fauna also extends in this direction; by this extension of the Polar Sea, east Asia was separated from North America. Consequently there was no land bridge.<sup>1</sup>

These conditions of Upper Jurassic times continued, according to Neumayr, into the Lower Cretaceous; the Wolga-stage, with its characteristic Aucella-beds, belongs in part to the Lower Cretaceous, and the Polar basin was also in the beginning of the Cretaceous in open communication with the northern Pacific. This is represented in Koken's map (1893, pl. 1), although Asia and North America approach each other considerably. This same map, however, expresses, for the Upper Cretaceous, a separation of the Polar Sea from the Pacific, and this land connection between Asia and North America is preserved in Koken's map for the older Tertiary (*l. c.*, pl. 2). The evidence for this disconnection of the oceans in the Upper Cretaceous time is given by Neumayr (1890, p. 389-391); palæontologically, we can trace a continuous Upper Cretaceous ocean, including the northern Pacific from California to Japan, which was connected with south India. This province differs strikingly from the American-European (Atlantic) province; the Polar Sea was much reduced in size, and, to all appearances, Siberia was largely dry land and was connected with North America.

Thus there is some evidence of the existence of a land connection between Siberia and Alaska, beginning at about the middle of the Cretaceous period, and continuing up to the end of the Tertiary. Whether this connection was continuous in time, or interrupted at certain periods, is hard to decide; at all events, it was of such a character that an easy and free communication was possible between the respective parts, and this is expressed very distinctly in the faunas of the northern land masses, although the

<sup>1</sup> This Jurassic ocean forms apparently the continuation of the old Triassic basin, comprising the Pacific and Arctic Oceans (see Neumayr, p. 266).

geological evidence is very slender on account of our defective knowledge of the Beringian countries.

For our present purposes, this has the following meaning. The *Potamobiidæ* of eastern Asia, the remnants of which are known as the subgenus *Cambaroides*, had easy access to northwestern America by way of the Beringian connection, from the beginning of the Upper Cretaceous to the end of the Tertiary. Since *Cambaroides* is to be taken, as we have seen above (p. 288), for the more primitive group, the migration must have been in an easterly direction. It cannot have taken place in recent times, since this way is now rendered impossible, and just this recent (or Pleistocene) interruption (probably connected with a change of climate) has separated the Asiatic and American range of *Potamobius*. Before the middle of the Cretaceous it was also impossible for the crayfishes to pass along this line, since then this connection was not yet formed, and thus we obtain a very important lower limit for this process in the dispersal of the *Potamobiidæ* about the *middle of the Cretaceous period*. Consequently, the *Potamobiidæ* may go back, in their geological history, at least as far as this time. We shall see later that we are able to define also an upper limit for the time of immigration into North America.

## 2. CONNECTION OF EASTERN ASIA AND AUSTRALIA.

Another geographic postulate of the distribution of the *Potamobiidæ* and *Parastacidæ* is the connection of east Asia, the region of *Cambaroides*, with Australia, the main region of the family *Parastacidæ*. This same connection, from Farther India and south China over the east Asiatic islands to north Australia, is suggested by the distribution of the subfamily of the *Potamonina*.

Other zoogeographical facts point the same way. Pilsbry (1894, p. xlv) says that eastern Asia and China, southward to Australia, constitutes a great division in *Helix* distribution, and many other writers have emphasized the close affinity of the fauna of Australia to that of southeastern Asia, although this is true only for certain groups of animals. The opposite opinion, which generally prevails, that Australia is sharply isolated from the rest of the world in its faunal relations, is founded chiefly on the highest forms of life, the Mammals. Other groups of animals, which permit us to draw conclusions in this respect, indicate clearly that a large part of the



Australian fauna is derived from Asia (see von Ihering, 1894, p. 406, and Hedley, 1899).

This connection between east Asia and Australia (Sino-Australian) is not well expressed in Jacobi's scheme. The apparent reason for this is that Jacobi considered chiefly those groups of animals (Mammals, Birds) which do not bear upon this question. Nevertheless, some of his "regions of dispersal" come under this head, namely, the ninth, tenth, eleventh and twelfth (Papuan, Farther Indian, Philippine, southern Japanese; see Jacobi, 1900, pp. 208-210), and discussing the Papuan, he directly mentions the Oriental origin of certain elements of it, thus indicating its relation to southeastern Asia.

Studying the tectonic configuration of the respective parts, we are to remember that Australia belongs to the old, Palæozoic Gondwana land of Suess (1888, p. 317 ff.), which also comprised Africa and India. But we cannot refer to this old connection of Australia with India, since India in turn was not then united with the rest of Asia, and since this connection was destroyed in very early times, possibly in Palæozoic. For a tectonic connection of Australia and eastern Asia (excluding India) we have only evidence to the contrary.

On the other side, the eastern parts of present Asia, especially China, northeastern Siberia, and Farther India, form a more or less complete tectonic unit. Suess (1888, pp. 206-242) has shown that this whole region consists largely of old archaic and palæozoic rocks, which form, in northern China, an old continental mass, in the south a series of folded mountain ranges (p. 287), which continue into the mountains of Tonkin and Anam as far as the mouth of the river Mekong. In this whole region no Mesozoic deposits (with the exception of Rhætic beds in Tonkin) are known. According to Koken,<sup>1</sup> a Triassic ocean extended from the region of the Himalaya mountains and Central Asia to the shores of the present Pacific, covering a large part of China. The latter may have been land before Rhætic times; but at present we have only evidence that it was surely land in the Jurassic period.<sup>2</sup>

<sup>1</sup> *Neues Jahrb. f. Mineral., etc.*, 1900, Vol. 1, p. 196.

<sup>2</sup> See Loczy, L. von, *Wissenschaftliche Ergebnisse der Reise des Grafen Bela Szechenyi in Ostasien*, Vol. 3, 1899; the Central-Chinese sea (south of the Kuen-Lun mountains) disappeared at the end of Triassic and in Jurassic times.

Thus it is clear that we may assume the existence of this continent, the Sinic, from the Jurassic upward.

Further, according to Suess, the chains of islands accompanying this old continent on its southern and eastern sides are tectonically connected with the latter. One of them is formed by the mountain ranges which form the Japanese and Philippine Islands, consisting of old rocks, and, in the south, we can trace a similar chain (Suess, 1885, pp. 579-588), which begins with the Burmese ranges, and extends over Malakka, Sumatra, Java eastward, possibly as far as New Guinea.

Thus, nothing in the tectonic configuration is opposed to the theory that at least a large part of the Indo-Malaysian islands belongs to the continent. But this does not give us any proof for an actual former connection of these islands with the Sinic continent. This can only be decided by geological investigation of the respective parts. Unfortunately, our knowledge in this respect is very scanty.

Neumayr (1890) constructs in his map, mentioned above, an old Jurassic continent, the *Sino-Australian*, which, with reference to eastern Asia, is well supported, and the Australian part of which is also established by the fact that large parts of Australia possess a very old age (Gondwana land). The connection of both goes over the present Indo-Malaysian Archipelago, and, according to the map, this region was largely land during Jurassic times. Further (Neumayr, 1890, p. 419), Australia became separated from Asia and the rest of the world before the end of the Mesozoic time, that is to say, probably in the Cretaceous. This same idea is expressed by Koken (1893) in his map of the distribution of land in the latter period. Here we see that Asia and Australia were disconnected during the Lower as well as the Upper Cretaceous, but Australia comprises parts of New Guinea and the Sunda Islands as far as Java, Borneo and the Philippine Islands. In the older Tertiary, Koken includes Farther India into Asia, but then follows an archipelago and Australia remains isolated.

This wide connection, drawn by Neumayr between Asia and Australia during the Jurassic period, does not seem to be well supported, since marine Jurassic deposits have been discovered in the region of the Malaysian islands.<sup>1</sup> On the other hand, it is settled

<sup>1</sup> In Borneo, according to Krause and Vogel (*Samml. geol. Reichsmus. Leyden*, Vol. 5, 1897). The so-called "old slates" of Borneo are said to belong to

that a number of these islands possess very old, possibly Archaic rocks, which are overlaid directly by Tertiary beds, thus giving evidence of an intervening extended land period, during which no sedimentation took place. This has been demonstrated for the Philippine Islands, where an Eocene, Miocene and Pliocene series follows on top of old crystalline schists.<sup>1</sup> Similar conditions are said to prevail in Java (Martin). This, however, seems to be doubtful, since Verbeck and Fennema,<sup>2</sup> although they do not positively deny the possibility of the existence of Archaic rocks, pronounce the schists of Java Cretaceous, upon which, unconformably, Eocene and younger Tertiary beds are deposited. Archaic rocks are found in the Island of Amboina, where they are overlaid by Tertiary and Quarternary coral limestones. Between both there are, locally, older sediments of undetermined age.<sup>3</sup>

Aside from the supposed Cretaceous schists in Java, we know of beds of this period in Borneo, and, according to Kossmat (1895, p. 469 f.), only such that belong to the Upper Cretaceous, corresponding to the Ariyalur group (Senonian) of India. This fact is the more important, since, as Kossmat points out, it demonstrates that the Upper Cretaceous of southern India can be traced over Assam and Borneo to Japan and the Island of Sachalin (and thence to the western coast of North America). This indicates a continuity of the oceans in this direction, and consequently *Australia and Asia must have been disconnected in the Upper Cretaceous.*

From the foregoing, the conclusion may be drawn, that the geology of the Indo-Malaysian Archipelago is too scantily known to form an adequate idea of the former connection of Australia and Asia. This much, however, is settled, that large parts of this archipelago were once land, and the single islands were in many cases connected with one another. Verbeck (*l.c.*) has shown that of the Island of Java, in Miocene time (that is to say, very late), only the western part existed as a unit, and that it was continued eastward by a series of small islands. At the end of the Tertiary these

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the Lias (Martin, *ibid.*, Vol. 5, 1898; see also Molengraaff, G. A. F., *Geologische Verkenningstochten in Central Borneo*, 1900).

<sup>1</sup> Martin, *ibid.*, Vol. 5, 1896.

<sup>2</sup> *Geologische beschrijving van Java en Madera*, 1897. See also Verbeck, in *Petermanns geograph. Mitteil.*, 1898.

<sup>3</sup> Martin, K., *Reisen in den Molukken, in Amboen, den Uliassern, Seran und Buru. Geolog.*, Teil 1, Leyden, 1897.

islands became connected, and the whole was united with the continent of Asia; subsequently, a new (Quaternary) subsidence took place. According to Weber,<sup>1</sup> Celebes was connected in early times (beginning of the Tertiary?) with eastern Asia, but was separated later and dissolved into smaller islands, and assumed its present form at the end of the Tertiary. If changes of this character took place during the comparatively short Tertiary period, we are to expect, in Pretertiary times, much more varied conditions, and it is by no means impossible that the different islands, of which certain parts (for instance central Borneo) were never submerged after the beginning of the Mesozoic era, were variously and repeatedly connected with each other and the Asiatic mainland.<sup>2</sup> Such changing conditions existed probably during the whole of the Mesozoic time, and it seems, on account of the scarcity of Jurassic deposits, that during the Jurassic period land-conditions prevailed, although the land may not have had the extent assumed by Neumayr. It may have been similar during the Cretaceous period, but it seems that the land bridge began to dissolve; at least, in the Upper Cretaceous, we have positive indications that the connection between Asia and Australia was interrupted. This bridge probably was never again completely restored; the single parts of it, however, were not stationary in Tertiary times, and communicated with each other in various directions. These changing conditions are noticeable as far as New Guinea, and, as regards the latter island, we know through Haddon, Sollas and Cole,<sup>3</sup> that it is closely connected, tectonically, with Queensland. The archaic and palæozoic rocks of the "Australian Cordilleras" continue across the islands of Torres Straits into the southern part of New Guinea, which belongs undoubtedly to Queensland, and was separated from it at a very recent period. On the other side, the larger Sunda Islands (Sumatra, Java, Borneo) must have also been united with the Asiatic mainland in very recent time, as is positively shown by their fauna of higher land animals.

<sup>1</sup> Weber, M., *Zool. Ergebn. Reise Niederlaend. Ost-Indien*, Vol. 2, 1892; Vol. 3, 1894.

<sup>2</sup> According to Molengraaff (*Geologische Verkenningstochten in Central Borneo*, 1900), Borneo was submerged in Precretaceous times, but part of it was land in the Middle Cretaceous. At the end of the Cretaceous a subsidence took place, then again an elevation. The different parts of Borneo were subject in various degrees to these changes, which continued through the Tertiary.

<sup>3</sup> *Trans. R. Irish Acad.*, Vol. 30, 1894.

If the first sharp separation of Australia and Asia belongs to the *Upper Cretaceous*, it is consequent, for the *Parastacidae* and *Potamobiidae*, that their area of distribution, which before the beginning of the Upper Cretaceous extended over the Sino-Australian continent, was cut in two; of course, the ancestral forms occupying this old continent could not possibly have been divided into these two families, and their differentiation was directly connected with this separation of the geographic range. After that, there was a chance for either family to develop, since there was no longer communication between the Asiatic and the Australian stock. This forces us to the conclusion *that the ancestors of these two families must have existed before the beginning of the Upper Cretaceous time*, and that during the Upper Cretaceous the division into *Potamobiidae* and *Parastacidae* took place. It is impossible to place the origin of these families at a later period, since, as we shall see below, any crayfishes of late Mesozoic or early Tertiary age, in any part of the world, belong either to the one or the other family. Although there was at least a partial connection of Asia and Australia in Tertiary times, the two families never came into contact again: with the cause of this remarkable fact we shall become acquainted below.

With reference to the *Potamoninae*, their distribution over the Indo-Malaysian Archipelago is only partly explained by the assumption of a former continuous land bridge. The distribution of the freshwater crabs is by no means simple, and does not extend uniformly from eastern Asia to Australia, but there are numerous complications and peculiarities. In the first line, we have to emphasize the fact that only a single group, which is apparently highly specialized, the subgenus *Geothelphusa*, reaches the continent of Australia, and that this group (in its typical forms) is restricted to the Indo-Malaysian islands, and is wanting on the Asiatic continent. This is the more remarkable, since this group is most abundant just on the large islands of Sumatra, Java, Borneo, and extends northward over the Philippine and Loo Choo Islands to Japan. On the other hand, we have seen that the typical species of the genus *Potamon* (subgenus *Potamon*), which are found in both India and China, reappear in very closely allied forms in Java, Sumatra and the Philippines, but do not pass farther to the East. Then again, the subgenus *Potamonantes* possesses scattered stations

(probably strongly discontinuous) as far as New Guinea, and the same is the case in the genus *Parathelphusa*.

For the present, these very strange conditions defy explanation, and especially the eastern boundary of *Potamon* (sens. strict.) and the western boundary of *Geothelphusa* are puzzling. But this much we may say, that the distribution of the *Potamoninae* over the Indo-Malaysian Archipelago is apparently due to the varying relations of the different islands between themselves and to the continents during the Tertiary period, and that it furnishes additional proof for the complexity of the changes that took place during this time in this region.

Another fact is to be especially mentioned. Among the *Potamoninae* we do not have such a sharp separation of Australian and Asiatic types as we have found among the crayfishes: on the contrary, the species of *Geothelphusa*, found in northern and eastern Australia, are all closely related to those found in New Guinea and on the other islands. Also the different forms of *Potamon* (sens. strict.), found in Java and Sumatra, are very closely allied to continental species. All this points to the conclusion that the separation of the respective parts from each other, which brought about the present conditions, must be of comparatively recent date, and that at a time not very far remote from the present the distribution of land and water in this archipelago must have been considerably different from what it is now. Thus it seems that the causes of the distribution of the *Potamoninae* in the Indo-Malaysian Archipelago are to be sought for in later times, presumably in the Tertiary, and that during this period, and possibly up to a very recent time, conditions prevailed here which—although they may not have amounted to a continuous land bridge—constituted a certain unstable connection between Asia and Australia. Probably there was a maze of larger and smaller islands, channels, straits and the like, which was not permanent in its parts, and changed repeatedly.<sup>1</sup>

Our final result on this question would be the following: South-eastern Asia was connected with Australia in the Jurassic, and probably also at the beginning of the Cretaceous period. In the

<sup>1</sup> According to von Ihering (1894, p. 406), Australia was connected with Asia during the Eocene and Oligocene. Hedley (1899) connects New Guinea with Australia in the later Tertiary; but a similar connection existed also in the Eocene, and through the latter Oriental elements were brought to New Guinea.

Upper Cretaceous, a sharp separation between both continents was formed, which continued possibly up to the Eocene. Then the connection was, at least partially, reestablished, but it was of a very changing character, which is expressed by the great complexity in animal distribution. These changing and unstable conditions prevailed all through the Tertiary, and up to the present time, and it is hard to trace them under the present imperfect state of our knowledge of the geology of the respective parts.

The Upper Cretaceous separation of Asia and Australia is expressed in the distribution of the *Potamobiidae* and *Parastacida*: the formerly continuous area of their ancestors, which comprised in the Lower Cretaceous the Sino-Australian continent, was divided, about the middle of the Cretaceous, in a northern (East Asia-*Potamobiidae*) and a southern (Australia-*Parastacidae*) part. The varying conditions of the Tertiary are expressed in the distribution of the *Potamonina*; the details, however, cannot be made out, and further study of the freshwater crabs of these regions, as well as a more thorough study of the geology of these parts, is very desirable.

### 3. CONNECTION OF AFRICA AND INDIA.

The occurrence of crayfishes (genus *Astacoides*) in Madagascar has led us, as we have seen above (p. 295), to the assumption that there once existed a connection of this island with southern Asia (respectively with the Sino-Australian continent). The same connection is suggested by the distribution of the *Potamonina*, of which the subgenus *Potamonautes* is found in Africa as well as India. The Madagassian forms of the *Potamoninae* (see above, p. 301) indicate a relation of this island to Africa, while a closer connection with India is not so striking. A genetic connection of the ranges of this subfamily in Africa and India by way of the Nile valley and Syria is improbable, although, geographically, this connection actually exists; this, however, is apparently due to secondary migrations, different branches of the subfamily, coming from India and Central Africa respectively, meeting in lower Egypt.

Thus we have to regard Madagascar as a stepping-stone between Africa and India, and, with reference to the *Potamonina*, its relation to Africa is closer than that to India.

This supposed connection is well known in zoogeography under the name of the *Lemurian* continent. Jacobi (1900, p. 169 ff.) quite recently has doubted this Lemuria-hypothesis, although he

introduces among his regions of dispersal, as a seventh, an Indo-African, which occupies this geographic position. He believes, however, that it is not correct to explain certain similarities of the faunas of India and Madagascar by a land-bridge, but prefers to accept the existence of a chain of islands, which permitted, in later Tertiary times, a migration of animals possessing the power of flight (Birds, Bats) in this direction. On the other hand, he grants a connection of Madagascar with Africa upward to the Miocene.

Jacobi's assumption of a series of islands instead of a continental connection from Madagascar to India seems to be well founded only for this particular time, the younger Tertiary. But the similarity of both faunas has apparently been underestimated by him, even if he takes into consideration only Mammals and Birds, and there are no doubt numerous relations between both parts among other animals not possessing the power of flight. This fact has been urged by Pilsbry (1894, p. xlv) for the *Helices*, and he says that Madagascar is much more closely allied to Ceylon and Australia than to South Africa.<sup>1</sup> The present cases offered by the genus *Astacoides* and within the family of the *Potamonidæ* are also very important for this question, since the idea of a migration of these forms over a chain of islands and across parts of the ocean is entirely out of question. Thus it seems that we have to assume a continental connection—if not during the later Tertiary—in earlier times.

The parts under discussion belong to the old Gondwana-land, which, according to Suess, existed in Palæozoic times, and was partially destroyed in the same period through the disconnection of Australia from it. Africa, however, remained intact, and formed an ancient table-land, to which was added as a peninsula the Lemurian bridge, which extended from Madagascar to India, and traces of which are preserved up to the Eocene (Suess, 1885, p. 538). This same peninsula is accepted by Neumayr for the Jurassic period, and is represented in his map; it is separated from the main part of Africa by a great gulf extending southward, the *Ethiopian Mediterranean Sea*, includes the present peninsula of India, and is not connected with the Sino-Australian continent, the Indian Gulf and the Strait of Bengal forming its northeastern shores. According to Neumayr (1890, p. 390), this Indo-Madagassian peninsula existed up to the end of the Cretaceous, and even

<sup>1</sup> In part, this may be due to old-Mesozoic, and even Palæozoic geography.



to the beginning of the Tertiary, but was destroyed in the older Tertiary (*l.c.*, p. 397).

The same view is expressed by Koken: for the Lower and Upper Cretaceous he gives to this peninsula about the same shape it had in the Jurassic (Neumayr), and in the older Tertiary he draws—instead of this continuous land-bridge—a chain of islands.

There are not many cases where we possess such ample evidence for the former existence of a land mass that has now disappeared, at least as regards such a remote epoch. The chief arguments for this land-bridge are taken from the character of the marine deposits found at the supposed southeast and northwest sides of this peninsula, and they are especially convincing for the Cretaceous period. The South-Indian Cretaceous, as it is found typically in the neighborhood of Pondichery, is known similarly developed in Madagascar and Natal, and belongs to the ocean to the east and south of this peninsula, while contemporaneous deposits of the western Indian Ocean (in East Africa) and in northwestern India are strongly contrasted to it, and are related to the Mediterranean type. We even may obtain further information as to the shape of this peninsula. According to Newton and Boule,<sup>1</sup> the Jurassic beds of the western coast of Madagascar belong to the Ethiopian Mediterranean Sea (possessing the Mediterranean type), while the Cretaceous beds (Cenomanian-Senonian) of the same parts exhibit the South-Indian type. This indicates that the Ethiopian Mediterranean Sea extended, during the Jurassic period, farther south than during the Cretaceous. The respective maps of Neumayr and Koken agree well with this: according to Neumayr, the southern extremity of Madagascar was united with Africa, while, according to Koken, the connection was situated at its northern end. This latter bridge continued to exist apparently during part of the Tertiary time. We have seen above that the connection of East Africa and India continued up to the very beginning of the Tertiary, and was destroyed soon after. This destruction, however, affected only the parts between Madagascar and India, while Madagascar itself remained connected with Africa: according to Jacob, up to the beginning of the Miocene. Lydekker<sup>2</sup> is of the opinion

<sup>1</sup> See review by Boehm in *Neues Jahrb. f. Mineral., etc.*, 1897, Vol. 1, p. 489.

<sup>2</sup> *A Geographical History of Mammals*, Cambridge, 1896.

that Madagascar became separated from Africa in the Oligocene or Miocene; at the same time he connects Madagascar with India, and believes that this connection was not severed before the beginning of the Pliocene. In opposition to this we maintain that the connection of Madagascar with India was interrupted before that with Africa.

As the only remnants of this old bridge, the Seychelles have been preserved. They consist, according to Bauer,<sup>1</sup> chiefly of granitic rocks, which are accompanied by dikes and sheets of volcanic origin. Only traces of sedimentary rocks are found, and these point to a very old age. While we thus may safely take the Seychelles for a remnant of this old bridge—and this is confirmed by the presence of the East-African genus *Deckenia*—the other islands of the Indian Ocean (Chagos group, etc.), are coral-formation. They may rest upon the highest peaks of the submerged Lemuria, but the latter itself has disappeared here. Consequently the fauna of these islands—at least as regards freshwater Decapods—does not contain any forms indicating this old bridge, since they must have all been drowned.

The northeastern extremity of the Indo-Madagassian peninsula was formed by the present peninsula of India. According to Neumayr and Koken, this latter was separated, from the Jurassic to the older Tertiary, from the rest of Asia, that is to say from the Sino-Australian continent, by the Strait of Bengal, and, during the older Tertiary, India was, according to Koken (*l. c.*, p. 452), an *island* (also disconnected from Madagascar). It seems, however, that this separation of India from the rest of Asia was not so permanent as is believed by these authors. It is true, as regards its tectonic configuration, India has nothing in common with Asia, but it seems that there was a connection, at least at certain periods.

That the "Central Mediterranean Sea" of Neumayr extended during the Jurassic period across northern India to the Bengal Strait, separating India and Asia, seems to be correct, since no evidence to the contrary has been brought forth, and the latest investigations have shown that Jurassic deposits are widely distributed not only in the western but also in the central Himalayas.<sup>2</sup> But during a part of the Cretaceous, this strait does not seem to

<sup>1</sup> *Neues Jahrb. f. Mineral., etc.*, 1898, Vol. 2.

<sup>2</sup> See Griesbach, *Rec. Geol. Surv. India*, 26, 1893, and Diener, *Verh. k. k. geolog. Reichsanst.*, 1895.

have existed. Already Meddlicott and Blanford (1879, p. lx) have doubted that the plain of the Ganges river was covered by the Cretaceous ocean, and, although these authors generally disbelieve the existence of such a strait during Jurassic, Cretaceous and Tertiary times, Diener (*l. c.*, 1895) has demonstrated that there exists, in the central Himalaya mountains, an almost complete series of sediments from the Cambrian to the Eocene, among which Triassic and Jurassic beds are well represented, while Cretaceous beds apparently are missing and Eocene again is known. This is very much in favor of a connection of India with Asia during the Cretaceous. A very positive opinion on this question is expressed by Kossmat (1895, p. 463). He says that the Middle and Upper Cretaceous ocean of southern and eastern India was *not* connected over northern India with Europe.

Therefore, it seems to be well to assume only for the Jurassic period and for the Lower Cretaceous a separation of India and the Sinic continent; that is to say, during these times Lemuria (Madagascar-India) was a peninsula connected with Africa. In the Middle and Upper Cretaceous, this peninsula became united with the Sinic continent, forming a land-bridge between the latter and Africa. This connection, however, was apparently interrupted again in Eocene times. According to Neumayr (*l. c.*, p. 481), the Eocene deposits of the Central Mediterranean Sea (Nummulitebeds) are continued across the whole of northern India to the Gulf of Bengal (and farther to Java, Borneo and the Philippine Islands), and indicate thus a continuous ocean, which isolated India from the rest of Asia. Since, at about the same time (Eocene), the destruction of the Lemurian bridge took place, India became an island, as is first pointed out by Koken. In Post-Eocene times, this strait separating India and Asia disappeared, and we have, in northern India generally, at about this time (certainly from the Miocene upward), a regression of the ocean (see Meddlicott and Blanford, 1879, p. liii). The island of India was definitively joined to Asia and never again separated.

After the destruction of the connection of India with Madagascar, in the beginning of the Tertiary, of the southwestern parts of Lemuria only Madagascar remained, which was still connected, as a peninsula, with East Africa. Then this connection was also severed, but not before the Oligocene or the beginning of the Miocene. Thus the main outlines of the present distribution of land

and water were established at about the beginning of the Miocene. After the destruction of the Lemurian bridge in the Eocene, its northeastern portion, India, became part of Asia, while its southwestern portion, Madagascar, which at first remained a peninsula of Africa, became an island.

The application of these geographical results to the distribution of the freshwater Decapods is the following: First, we have to emphasize that before the middle of the Cretaceous it was impossible for the genus *Astacoides* to reach Madagascar. Since the separation of the Asiatic and Australian group of the crayfishes took place in about the Upper Cretaceous and since the morphological differentiation of the *Potamobiidae* and *Parastacidae* was connected with this separation, and further, since *Astacoides* must have immigrated into Madagascar from the Asiatic part of the old Sino-Australian continent, this latter process must have gone on shortly before the completion of this separation, that is to say, about the middle of the Cretaceous. This assumption is supported by the morphological characters of *Astacoides*, which are, in a certain degree, intermediate between the present two families and favor the view of an early separation from the original stock.

Thus there is nothing that prevents us to assume an immigration of *Astacoides* from southeastern Asia into Madagascar in the middle of the Cretaceous period. At a later time this does not seem to have happened, since, in this case, we should have different morphological characters in *Astacoides*. At an earlier time this immigration was impossible, since then India was not connected with the Sino-Australian continent. After the Eocene this migration was absolutely impossible, since then the land connection between India and Madagascar had disappeared.

Although we may thus fix the time of immigration of *Astacoides* rather exactly, there arise other questions. We want principally an explanation of the absence of similar forms in Africa itself, and for the absence of such in India and generally in southeastern Asia.

Regarding the *Potamoninae*, their presence in Madagascar, and the close relation of the Madagassian forms to East-African, is easily explained by the former connection of Madagascar with Africa. The freshwater crabs of Madagascar thus indicate geographical conditions which are older than Miocene. The presence

of *Deckenia* on the Seychelle Islands connects also this group more closely with Africa than with India. Possibly this connection is identical with that over Madagascar, although *Deckenia* has not been found on the latter island.

The presence of *Potamonina* in India, corresponding to the African type (subgenus *Potamonautus*), indicates the full development of the Lemurian peninsula, that is to say, conditions prevailing in the oldest Tertiary, if not earlier. *Potamonina*, represented by forms which resembled the subgenus *Potamonautus*, must have existed at least in the beginning of the Eocene, and their distribution extended over Africa and the Lemurian peninsula, including India. During the Eocene this range was separated into two parts, an African (to which Madagascar belonged) and an Indian, and, beginning in the Miocene, the *Potamonina* had a chance to expand over southern and eastern Asia (Farther India and China<sup>1</sup>). At the same time they availed themselves of the various and changing connections within the region of the Indo-Malaysian archipelago, occupying the latter and reaching Australia. The opening of this region of dispersal offered to this group a new opportunity for a rich development, and the origin of the subgenera *Potamon* and *Geothelphusa* was probably the outcome of it.

We cannot leave this chapter without saying a few words on the Arabian region of dispersal of Jacobi. This extends from northeastern Africa across Arabia to India. Jacobi mentions the similarity of the Siwalik-fauna of India with the Ethiopian. This, consequently, refers to a very recent period, the later Tertiary. Before this time, in the older Tertiary and in the Mesozoic, this connection is out of question. The *Potamonina*, which, as we have seen, existed in the older Tertiary, show no trace of this connection across Arabia, and, as we shall see below, our knowledge of the ancient geography of these parts is a very fair one. Arabia itself formed originally a part of Africa, and the Red Sea did not exist at all in the earlier Tertiary, it being quite recent (see below). Toward the north, northeast and east Arabia was circum-

<sup>1</sup>There was, possibly, an earlier chance to reach the Sinic continent, in Upper Cretaceous times, and I am inclined to believe that the discontinuous localities of *Lotamonautus* (and *Parathelphusa*) in the Indo-Malaysian archipelago point to an immigration of these forms that precedes in time that of *Potamon sens. strict.*

scribed by sea—the Central Mediterranean Sea and the Ethiopian Gulf of Neumayr. A connection with India in this direction, and a migration of *Potamonina* from India to Africa (or *vice versa*) by this route was then impossible.

Further, I should like to point out that we have to be careful about this Indo-Madagassian bridge. A case which has occurred to me, and which might lead to misinterpretation, is furnished by the distribution of the Reptile-family *Chamaeleontidae*. According to Gadow,<sup>1</sup> this family is found in Africa, Madagascar and India, a distribution which is quite analogous to that of the *Potamonina*, and might induce us, at the first glance, to trace it back to this old Indo-Madagassian connection. A closer study, however, reveals the fact that the *Chameleon* of India has nothing to do with the Madagassian species, but is related to the form widely distributed in North Africa, Syria and Asia Minor. Here the connection apparently goes from North Africa over Syria and Arabia to India, and this distribution belongs to a much later period when Lemuria no longer existed.

#### 4. CONNECTION OF NEW ZEALAND WITH AUSTRALIA.

We have seen that a genus of the family *Parastacidae*, *Paranephrops*, is found in New Zealand, and this fact points to a former connection of these islands with Australia. We further are to pay attention to some additional facts, which, although they do not seem to be sufficiently established to be accepted without comment, are apt to throw some light upon this connection.

First, according to Huxley (*Tr. Zool. Soc.*, 1878. p. 771), *Paranephrops* is said to be found in the Fiji Islands. This locality is supported by two specimens in the British Museum, which are in a very bad condition; moreover, there is no report as to the authenticity of the locality, and the genus has never again been reported from these islands.

Further, Nobili (1899) describes from southern New Guinea a genus and species, *Astaconephrops albertisi*, which is said to be closely allied to *Paranephrops*. It is impossible, however, to control the systematic position of this form, since only external characters are given, and the most important one, the branchial

<sup>1</sup> Gadow, H., "Amphibia and Reptilia," in *The Cambridge Natural History*, Vol. 8, 1901, map, p. 568.

formula and shape of gills, is entirely unknown; a figure of this very important form is also missing.

But taking it for granted that the genus *Parastacus* itself is found in the Fiji Islands, and that *Astaconephrops* in New Guinea is closely allied to it, this would indicate a connection of New Zealand with Australia by way of Fiji Islands and New Guinea. This assumption appears, judging alone from this material, very poorly supported, but it agrees well with other known facts which have led to a similar theory.

According to Hedley (1899), New Zealand was connected with Australia in the following manner (see map, *l. c.*, p. 404). From North Australia and New Guinea, which were united, a peninsula extended over the Solomon Group and the New Hebrides, where a smaller peninsula branched off in the direction toward the Fiji Islands; and, farther, this main peninsula extended over New Caledonia, Lord Howe Island to New Zealand. Hedley calls this the "Melanesian Plateau," and we may name it conveniently the Melanesian Peninsula or *Melanesia*. As to the time of existence of the latter Hedley does not express himself very positively, but according to von Ihering (1894, p. 406), New Zealand and the Fiji Islands became separated from Australia before the Eocene, or, as may be gleaned from other places in his text, at the beginning of the Eocene.

The views of these two authors are founded exclusively upon zoogeographical evidence, and we see that the genus *Paranephrops* of New Zealand is apt to furnish additional support to Hedley's Melanesian Peninsula. That this peninsula was disconnected from Australia, not later than in the Eocene, also agrees with our material. We have seen above that forms of the *Parastacoid*-type must have existed in Australia as early as in the Upper Cretaceous, and thus nothing opposes the assumption that they immigrated into New Zealand in Pre-Eocene times.

Examining the tectonic and geological side of the question, we have to refer first to the views propounded by Suess (1888, p. 181 ff.). According to him, the Alps of New Zealand are a comparatively old range, which existed probably as early as in Jurassic times, and, further, he points out (*l. c.*, p. 203 ff.) the analogy in the structure of New Caledonia and New Zealand. For the rest, the islands between New Caledonia and New Guinea are too poorly known in this respect, and, therefore, we cannot say anything

about a possible tectonic connection of these parts. Neumayr, however (1890), draws in his map of the Jurassic continents, mentioned repeatedly above, a peninsula, which is connected with his Sino-Australian continent, and which corresponds closely to Hedley's idea of Melanesia. This peninsula is missing in Koken's map (1893) of the Cretaceous continents, and even New Zealand is not given as land there. But Koken does not seem to have paid much attention to these parts of the earth's surface in Cretaceous times, since it seems quite sure that at least parts of New Zealand were land then. In the Older Tertiary, New Zealand and New Caledonia were islands, according to Koken, while Australia extended far to the east, including Lord Howe Island.

Although, in general, the geological evidence for the connection of New Zealand with Australia is very scarce, we certainly have to assume it according to the characters of the fauna and flora of New Zealand, and the material at hand points distinctly to the fact that this connection was interrupted at a comparatively early period. Thus there is nothing that is opposed to the view of von Ihering, that the final isolation of New Zealand took place not later than the beginning of the Eocene, and there is no objection to the demonstration on the part of Hedley that this connection with Australia was by way of New Caledonia and New Guinea. Our present case, the distribution of *Paranephrops* in New Zealand, fits well into this theory: this genus reached New Zealand in Pre-Tertiary times, probably in the Upper Cretaceous, and very likely by the way indicated by Hedley; since the Eocene it has become isolated on this island group.

##### 5. CONNECTION OF SOUTH AMERICA WITH AUSTRALIA (RESP. NEW ZEALAND).

The genus *Parastacus* in the temperate and subtropical parts of South America points to a connection of this continent with those parts in which allied forms are found, namely, with Australia and New Zealand. Numerous instances of a similar distribution, which suggest a relation of the same parts, are known, not only among land and freshwater animals, but also among the marine littoral fauna. This remarkable fact has been noticed at a very early time, and has suggested various theories, which have been reviewed and classified by the present writer (Ortmann, 1901). The views of the majority of the later authors now agree more or



less in that this connection is placed across the Antarctic continent, and this idea is chiefly supported by Hedley (1895, 1899), von Ihering (1891, 1894), Osborn (1900), Pilsbry (1894), and Ortmann (1901, 1902).

While Pilsbry only generally expresses the opinion that the supposition of an old Antarctic continent connecting the respective parts of the present southern continents would furnish the conditions necessary for the explanation of the zoogeography of the land-mollusks, and while Osborn only tries to give an approximate idea of the mutual relations of these land-masses by pointing out that a subsidence of the ocean level of a certain amount would connect these parts, von Ihering (1894, p. 438) gives a more detailed theory of this connection. He unites not only South America over Antarctica with Australia, but continues this (Mesozoic) land mass beyond the Indo-Malaysian islands to east Asia, thus including the Sino Australian continent discussed above. He calls this vast continent by the name of *Archinotis*.

As to the details of the special connection of Australia and South America, Hedley's opinion is the most important; according to him (1895, p. 6), during Mesozoic and older Tertiary times a stretch of land extended from Tasmania over the South Pole to Terra del Fuego; the shore line of this land (Antarctica) formed a wide gulf between Tasmania and Cape Horn, and approached the Pole. This land-bridge, however, was not very solid, but was subject to various changes resulting in a repeated breaking up and becoming reunited of the different parts. As regards New Zealand, he believes that during the Tertiary time it was not directly connected with Antarctica. In another paper, however (1899, p. 399), Hedley also assumes a connection of New Zealand with Antarctica, but this was of an older date than that from Australia over Tasmania to Antarctica, and consequently is to be placed in the Mesozoic time.

That Australia was once connected with Antarctica, especially with what is now called Wilkes' and Victoria Land, can be imagined as possible on tectonic grounds. Australia itself consists, according to Suess (1888, p. 188 ff.), in its eastern part of a very old range of mountains, running in a north-southerly direction; its larger western part is an old Archaic and Palæozoic plateau (part of Gondwana Land). Both parts are fractured and cut off toward the south, and the southern parts have disappeared; a line

of faults at the southern margin of the Australian Plateau indicates that Australia undoubtedly extended once farther southward, in the direction toward Antarctica. Whether it was really united with the latter cannot be said positively, chiefly because the geological structure of Wilkes' Land is entirely unknown.

The time of the subsidence of the southern parts of the old Australian continent can be determined according to the conditions known to exist on the shores of the great Australian Bight. Here, on the foot of the broken edge of the Australian Plateau, a series of Tertiary deposits is found, the age of which is not yet positively ascertained, but which seem to belong to both the older and younger Tertiary. The fact that no older (Mesozoic) beds are found in this region seems to indicate that such were not deposited, and that means to say that up to the end of the Mesozoic time the southern part of the Australian Plateau had not subsided, and that this process took place at the very beginning of the Tertiary.

Thus we have reason to believe that the connection of this part of Australia (the western plateau) with Antarctica *existed up to the end of the Mesozoic time.*

The Tertiary deposits of the south coast of Australia are lacking from Tasmania along the eastern coast of Australia; here is a fracture toward the south and east, the age of which cannot be determined at present. Hedley believes that there was here a connection with Antarctica that persisted up into the Tertiary (over Tasmania), but he gives no geological evidence for it. It is entirely unknown whether the East Australian Cordilleras find a continuation in Antarctica. So Hedley's assumption may or may not be correct.

Another tectonic line in these regions has been pointed out by Gregory.<sup>1</sup> He also emphasizes the former southward extension of the Australian Plateau; but besides, there seems to be, according to him, a very important tectonic line marked by the volcanoes of New Zealand and Victoria Land, and this, possibly, finds its continuation in the volcanoes of the region of Graham Land, and passes thence over Terra del Fuego to the South American Cordilleras. Of course, this is no evidence at all that this line from New Zealand over Antarctica to South America has ever been a continuous mountain range actually connecting these parts, but the

<sup>1</sup> *Nature*, Vol. lxiii, 1901, pp. 610-611, with map, p. 611.

existence of such a line would in a large degree facilitate the imagination of such a connection, and would force us—if we have other evidence pointing to a former connection of these parts—to construct this old land-bridge nowhere else but along the direction of this line. That is to say, the connection of Australia and New Zealand with South America, which is probable on account of certain facts in the distribution of life, *was across the Pole, and not in lower latitudes in the southern part of the Pacific Ocean*, as accepted by some authors.

The tectonic connection of Graham Land with Terra del Fuego, indicated by Gregory, is much emphasized by Fricker.<sup>1</sup> According to him, it is formed by the arc of islands running from Terra del Fuego over South Georgia and the South Sandwich Islands to Graham Land. This line, however, again indicates only the general direction of this possible connection, but does not give any hints as to its actual existence, nor to the possible time of it.

We know that a large part of South America (the Brazilian Plateau, see below) is a very old continental mass, which extended southward into northern Argentina, but not into Patagonia. What is now the chain of the Cordilleras was certainly ocean during Mesozoic times, since here we find Jurassic and Cretaceous deposits largely developed, and the latter have been traced far to the south and over almost all of Patagonia; the Tertiary beds of southern Patagonia rest, wherever this has been observed, upon Cretaceous deposits.<sup>2</sup> The Patagonian Cretaceous, in its upper divisions, consists of rocks formed apparently under continental conditions (littoral, freshwater, or eolian), and these latter (Guaranitic beds) were subject, after their deposition, to erosion, indicating a land period at the close and after the Cretaceous. Thus, there seems to have been an upheaval, beginning at the end of Mesozoic time and continuing into the Tertiary; during the Eocene these regions probably were land to a large extent.<sup>3</sup>

West of the Mesozoic beds known in the tract of the Cordilleras there are, in the so-called Coast Cordilleras of Chili, rocks of another character; they are apparently metamorphic, but their age is disputed. According to Steinmann,<sup>4</sup> they are Mesozoic; and

<sup>1</sup> *The Antarctic Regions*, London, 1900, p. 140 ff.

<sup>2</sup> See Hatcher, J. B., in *Amer. Jour. Sci.*, Vol. ix, 1900, p. 95 ff., and Ortmann, *Rep. Princeton Exped. Patagonia*, Vol. iv, Part 2, 1902, p. 285.

<sup>3</sup> See Ortmann, *l. c.*, p. 317.

<sup>4</sup> *Neues Jahrb. f. Mineral., etc.*, Beil., Bd. 10, 1895, p. 6.

according to Wollf,<sup>1</sup> they are at least older than Jurassic. This coast range is continued southward across the Straits of Magellan, and forms the southwest and south coast of Terra del Fuego, where similar rocks are found, and here it curves more and more in a west-easterly direction.

However, the old and even Mesozoic age of the rocks composing this chain is not generally accepted, and also the identity of the Fuegian rocks with those of Chili has been doubted; Norden-skjöld,<sup>2</sup> for instance, takes the metamorphic rocks of the outer (western and southern) side of Terra del Fuego for Cretaceous.

Thus we see that there is considerable uncertainty about the configuration and geology of southern South America in the Mesozoic era; but this much seems to be settled, that the Chilean coast range existed as early as the Cretaceous period,<sup>3</sup> and that the Cordilleras in Terra del Fuego were not formed later than in the Cretaceous. It is just this latter chain that continues over Staten Island, South Georgia, etc., and finally connects with Graham Land; and if there was connection at any time, it was by this way and in the Cretaceous.

Further, there is no doubt that at the end of the Cretaceous period large tracts of Patagonia became dry land, and the maximum of land extension falls probably in Eocene times.

Consequently we have to put the chief connection of the southern parts of South America with Antarctica at the end of the Cretaceous and in the Eocene. But we are to emphasize here that thus far we have been able only to connect the Chilean coast range with Antarctica. According to von Ihering, this connection also comprised old Archiplata (the Brazilian mass) and existed during

<sup>1</sup> Wollf, F. von, in *Zeitschr. deutsch. Geolog. Gesellsch.*, Vol. 51, 1899.

<sup>2</sup> Geological Map of the Magellan Territories (Svenska Exped. till Magellans-land, Vol. 1, No. 3, 1899).

<sup>3</sup> And possibly earlier. Burckhardt, C. ("Traces géologiques d'un ancien continent Pacifique," in *Rev. Mus. de la Plata*, Vol. 10, 1900, p. 177 ff.), has brought forth some evidence for the assumption that in Chili, west of the present Cordilleras, which were sea during the Upper Jurassic, there existed a continent, the eastern shore of which was formed by the Chilean coast range. There is no means, however, of deciding how far this Jurassic continent extended to the west. The Jurassic age of this range, together with the corresponding rocks of Terra del Fuego, etc., is quite likely if Gregory's theory of the tectonic connection with New Zealand is correct; also, the mountains of New Zealand are said to possess Jurassic age (see above, p. 334).

the whole Mesozoic era, but this seems to be doubtful; at any rate, a connection of the southern and western land in South America (Chilean coast range) with the rest of South America is improbable during a large part of the Cretaceous time, since marine deposits belonging to this period are found in the present Cordilleras, indicating separation by sea. This sea apparently was a strait running in a north-southerly direction, and coinciding approximately with the present direction and location of the Cordilleras. This strait became dry at the beginning of the Tertiary, in the Eocene, since Tertiary deposits are not found here, and thus a connection of the main mass of South America, the Brazilian Plateau, was formed in an east-westerly direction with the Chilean coast range. This completed the connection of South America with Antarctica in Eocene times, and, in our opinion, is very important and serves to explain the numerous zoogeographical peculiarities of South America.

To sum it up, we are justified to draw the following conclusions: There is nothing that opposes, on tectonic or geological grounds, the assumption of a connection of *Australia with Antarctica*, as far as the evidence at hand goes. *This connection belongs pre eminently to the Mesozoic time*, and was interrupted, at least for a large part, at the end of this era, definitively at the beginning of the Tertiary. We have no positive evidence for a *permanent Mesozoic connection of South America and Antarctica* (but such may have existed); *but a connection of these parts is very probable at the end of the Mesozoic time, and especially during the Eocene between the Antarctic lands and the old Brazilian mass*; the southernmost parts of South America (southern Patagonia and Chili) were connected in the Cretaceous with Antarctica, forming part of it, but were still separated from Archiplata. In the Eocene they were also connected with the latter. This latter union was brought about by the upheaval of the Cordilleras, which began toward the close of the Cretaceous and continued almost all through the Tertiary.

We are not going to follow up this idea any further, although we believe that it will prove to be very important with regard to the origin of the South American fauna. For our present purpose, the explanation of the presence of the genus *Parastacus* in South America, we arrive at the conclusion that the family *Parastacidae*, which existed, as we have seen, during the Upper Cretaceous period in Australia, had a chance, during this same time, to spread

into Antarctica, and consequently into the southernmost parts of America (Chili). Thence it extended, in the beginning of the Tertiary, into Northern Argentina and Southern Brazil (Archiplate). This west-easterly direction of migration from Chili to Brazil is in a certain degree expressed in the present distribution of the genus *Parastacus*, and the distribution of the genus *Eglea* seems to have been formed under similar conditions, although its Antarctic origin does not seem probable. The present southern boundary of *Parastacus* is possibly due to the present climatic conditions, it having died out in the south of Chili and Patagonia on account of the unfavorable climate of these parts.

The fact that the genus does not extend northward into the truly tropical parts of Brazil needs further explanation. We shall return to this later.

The presence of the genus *Parastacus* on both slopes of the Cordilleras (even the identical species is found in one case on both sides, and in this respect the genus *Eglea* agrees with *Parastacus*) points to a time when the Cordilleras had not yet attained their present elevation. As v. Ihering has shown, for many groups of animals this chain forms a very sharp barrier, and it does not seem probable that these freshwater Crustaceans are able to cross these high snow and ice-covered mountains. In the case of *Parastacus agassizi* a shifting of the continental divide (by the capturing of the headwaters of a stream belonging to the drainage of the opposite side) cannot explain its presence on both slopes, since in this region the original divide seems to be intact (the waters of Lake Nahuel Huapi drain to the Atlantic Ocean). Thus also this fact is in favor of an early origin of the distribution, since the elevation of the Cordilleras, although beginning at the end of the Cretaceous, did not attain its maximum till about the Miocene.<sup>1</sup>

#### 6. CONNECTION OF THE WEST INDIES WITH CENTRAL AND SOUTH AMERICA.

We have seen above that *Cambarus cubensis* of Cuba finds its most closely allied species in *C. mexicanus* of Mexico. Similar conditions prevail among the species of *Pseudothelphusa* from the Greater Antilles, two species (*P. americana* and *terrestris*) being also found in Mexico. On the other hand, the six species of the

<sup>1</sup> According to Hatcher, the Miocene Patagonian and Santa Cruzian beds are largely disturbed in the region of the Cordilleras in Southern Patagonia.

genus *Epilobocera* (from Cuba to Porto Rico and Sta. Cruz) are restricted to these islands and do not possess any closely allied forms on the mainland, although there is no doubt that they are distantly related to the Central and South American freshwater crabs and must have been derived from these parts. Thus it seems that we are to distinguish two groups among the freshwater Crustaceans of the Greater Antilles, pointing to two migrations from the mainland of Central America—an older one, represented by *Epilobocera*, the higher age of which is supported by the fact that this genus possesses in some respects the most primitive characters among the whole subfamily, and a younger migration, represented by the identical species of *Pseudothelphusa*. It is doubtful to which of these groups *Cambarus cubensis* belongs, since it is different from but closely allied to a Mexican species.

Entirely different in its relations is the *Pseudothelphusa* (*P. dentata*) of the Lesser Antilles. This one points beyond doubt to South America (Trinidad and Venezuela) and bears no relation at all to the Greater Antilles, not to speak of Mexico.

The geology and tectonics of the West Indies and Central America are only poorly known, but lately some very important contributions have been published. Nevertheless, the conditions prevailing here are far from being clear, and the opinions of different authors vary frequently. This much seems to be sure, that the history of this section of the earth is a very varied and complex one.

In the first line we are to consider the fact that the general features of the main mountain ranges of Central America and the West Indies possess much in common and differ sharply from both North and South America. Especially the west-easterly strike of the old ranges of Central America (Guatemala, Honduras), as well as of the Greater Antilles (Cuba, Hayti, Porto Rico, Jamaica), is very remarkable (see Suess, 1885, p. 698 ff.), and indicates a former tectonic unit. According to Hill (1898), old rocks exhibiting the same west-easterly strike are found largely distributed also in Nicaragua and Costa Rica, and, further, in the region of the Isthmus of Panama, especially to the east of Colon, in the Cordilleras of San Blas. Furthermore, the whole northern shore of Venezuela, from Puerto Cabello to the northeastern end of the island of Trinidad, consists of old granitic ranges with the same strike. All these observations, although apparently incomplete and scattered, most likely

indicate that this whole region, *i.e.*, Central America, the Greater Antilles and the northern coast of South America, possesses an "old basement of granitic rocks of earlier age than the oldest determinable sedimentary rocks" (Hill, 1898, p. 241), which, in its west-easterly strike, differs entirely from the present mountain ranges of North and South America, and it is possible that these parts once formed a unit, a solid continental mass. As to the age of this continent we may form an idea if we consider that (Hill, *l. c.*, p. 243) Jurassic beds are absent in this region, so that during this time at least this continent was in existence. The same seems to be true for a large part of the Cretaceous time. Cretaceous deposits are wanting in Central America from Costa Rica eastward in the Isthmian region and on the West Indian islands.<sup>1</sup> On the other hand, Cretaceous beds are found in Guatemala to the north of the old granitic mountains. They are also extensively developed to the south and southeast of the old granites in Colombia and Venezuela (see below), and thus it seems that this old continent was washed to the north as well as to the south by Cretaceous seas.

But at about this time (toward the end of the Cretaceous) this old Mesozoic Antillean continent must have been destroyed, probably by the formation of the Caribbean Sea. We do not know much about the exact time when this happened, but we know that the subsidence forming this basin within this old mass was accompanied by a faulting along the margins of the subsiding area. This fault is clearly seen at the coast of Venezuela, where, according to Suess (1885, p. 687 f.), the old coast range breaks off to the north. The fact that within the whole region of the Caribbean Sea no Cretaceous deposits are positively known makes it very probable that the formation of this depression falls at the end of the Mesozoic age.<sup>2</sup>

<sup>1</sup> There are, however, Pre-Tertiary sediments, belonging possibly to the uppermost Cretaceous, in some of the Greater Antilles (see Hill, *Amer. Journ. Sci.*, Vol. 48, 1894, p. 197); but this again demonstrates that sedimentation in these parts did not begin till the very end of the Mesozoic time.

<sup>2</sup> There are Cretaceous deposits of Lower Senonian age in western Venezuela which possess the Mediterranean type (see Gerhardt, in *N. Jahrb. Mineral.*, etc., Beil., Bd. 11, 1897, p. 87). This possibly is the first indication of the existence of the Caribbean Sea. But we must not forget that the Lower Cretaceous of Colombia and Peru also exhibits Mediterranean character, which is due, no doubt, to the Orinoco connection. It is remarkable that the relation of these Lower Cretaceous beds to Texas is not very evident, they probably being sepa-



In subsequent times, at the beginning of the Tertiary, the Caribbean Sea must have existed, since Tertiary deposits are largely developed in this region, not only on the Antilles but also on the Isthmus of Panama. It seems that in the beginning of the Tertiary the old Antillean continent was divided into two main sections—the Greater Antilles with Honduras and Guatemala to the north, and the coast range of Venezuela to the south. The remnants of this continent in the Greater Antilles and Central America remained first in a large part land, but apparently they were subject to various changes during the Tertiary period and subsided and were elevated repeatedly.

We have seen that the geographical distribution of certain freshwater Decapods demands in the first line a connection of the Greater Antilles with Mexico, and according to the foregoing considerations this connection can have been situated only in the direction over Honduras and Guatemala. We have further seen that a Mesozoic connection of these parts is very likely, and that the connection of Venezuela with Central America existed almost up to the end of the Cretaceous. As we shall see below, we have reason to believe that the freshwater crabs reached Venezuela in the second half of the Cretaceous, and consequently it was also possible for them to extend during this time into Central America (and Mexico). If the latter parts were then or later connected with the Greater Antilles, this would account for the presence of the most primitive genus of the subfamily, *Epilobocera*, in these islands. On the other hand, *Potamobiidae* were probably present at the end of the Cretaceous times in western North America. These parts were connected with Central America in this period, Mexico being dry land, and thus there was also a chance for the *Potamobiidae* (represented here by *Cambarus*) to reach finally the Greater Antilles. Therefore we reach the conclusion that the first immigration of freshwater Decapods into the Greater Antilles, represented by *Epilobocera*, belongs to the end of the Cretaceous or the beginning of the Tertiary, and that *Cambarus cubensis* possibly also belongs to it; but since this form is a true *Cambarus*, although a primitive one, I should prefer to put its immigration rather in the Tertiary than in the Cretaceous.

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rated from Texas by the Antillean continent, while the Upper Cretaceous of Western Venezuela shows close affinity to Texas, the Antillean continent having disappeared.

N.B. The same zoogeographical question has been investigated by Simpson<sup>1</sup> with reference to the land and freshwater Mollusks. He points out that among this group in the Greater Antilles we find quite a number of species which are identical with species from Central America and Mexico (list p. 488, *l. c.*), and, besides, there are in both parts numerous and more or less closely allied forms. Simpson does not distinguish very sharply these two categories, identical and allied forms, but they correspond very likely to the same two groups among our Decapods.

Now Simpson draws the following conclusions: Sometime during the Eocene the Greater Antilles were elevated and connected with each other and with Central America by way of Jamaica (and possibly across the Yucatan channel). Then a period of subsidence followed, culminating in the Miocene and submerging the Antilles with the exception of their highest parts, which ended the connection with Central America. In Postmiocene times the Greater Antilles were elevated again and attained their present shape.

For the Lesser Antilles the matter was entirely different. These islands did not exist at all in Eocene times or were submerged subsequently, since their Mollusk-fauna, with the exception of a few forms which may have reached them by drift, shows no affinities to that of the Greater Antilles. After the formation of this island chain, during the course of the Tertiary,<sup>2</sup> it was populated chiefly from South America, and, as Simpson believes, by drift. The South American (Venezuelan) origin of the fauna of the Lesser Antilles is also confirmed by our material. *Potamocarcinus dentatus* points directly to Trinidad and Venezuela and not to the Greater Antilles. I should doubt, however, that this species has reached these islands by drift, and I am inclined to assume a continental connection of these parts, which may have been of short duration, during the later Tertiary. I am loath to believe that it is possible for these freshwater crabs to be transported across salt water, and the fact that one species is found on the islands of Guadeloupe, Dominica, Martinique, St. Lucia, another in Trini-

N.B. <sup>1</sup> Simpson, C. T.: "Distribution of the Land and Freshwater Mollusks of the West Indian Region, and their Evidence with regard to Past Changes of Land and Sea" (*Pr. U. S. Nat. Mus.*, Vol. 17, 1895).

<sup>2</sup> That these islands were formed during the Tertiary is also the opinion of Hill. See Report by Robert T. Hill on the volcanic disturbances in the West Indies in *The Nation. Geograph. Magaz.*, Vol. 13, 1902, pp. 229, 240, 265.

dad and a third in Venezuela is entirely opposed to the drift theory, since under the latter we ought to expect only *one* species in this whole region.

Simpson's theory of the origin of the West Indian faunas is supported exclusively by zoogeographical evidence, and, as we have seen, it agrees admirably with the facts presented by the Decapod Crustaceans. But the various changes undergone by the West Indian islands have been investigated also from a geological and physiographical standpoint. I shall disregard the views of Spencer<sup>1</sup> on the Antillean continent, which are certainly exaggerated, since he makes this whole region land during the Pliocene, even including the floor of the Mexican Gulf and the Caribbean Sea. According to him, the Pliocene land would have been elevated above the present level to the amount of one and one-half to two and one half miles, and this would result in a wide connection of both North and South America with the Antillean land. But this is simply impossible. If such a land connection had existed in Pliocene times, it should have left not only unmistakable traces in the present fauna of the Antilles, but the Antillean fauna ought to be practically identical with that of the southern parts of North America and the northern parts of South America; but this is by no means the case. Nevertheless, one of the items in Spencer's theories is important for our purposes. This is the assumption of a Pliocene elevation of these parts, succeeded by the opposite movement at the end of the Pliocene and in the Pleistocene.

On the other hand, Hill<sup>2</sup> assumes for Cuba a subsidence at the beginning of the Tertiary. This is followed, in the older Pleistocene, by a rapid elevation, continuing more or less continuously up to the present time. This late Tertiary and recent elevation influenced also the neighboring parts of the Gulf of Mexico and the Caribbean Sea, and Hill concedes that it was possible that Cuba extended then as far as Yucatan, thus connecting with Central America.

The views of Hill and Simpson agree only in part as to the general movements of these regions. Simpson assumes an Eocene elevation and land connection, while Hill's elevation is Pleistocene. But it is quite possible that both are correct. We have

<sup>1</sup> Spencer, J. W.: "Reconstruction of the Antillean Continent" (*Bull. Geol. Soc. America*, Vol. 6, 1895).

<sup>2</sup> *Bull. Mus. Harvard*, Vol. 16, 1895.

seen that our material points to a double connection of Cuba and Central America, an older and a younger one, and it is very likely that the one is identical with Simpson's and the other with Hill's. Between them there is a period of subsidence, the maximum of which belongs probably to the Miocene. This agrees with both Hill's<sup>1</sup> and Simpson's views. The upheaval assumed by Hill for the end of the Tertiary and the corresponding connection with the mainland has been indicated previously by Neumayr (1890, p. 541), and the same theory is proposed by Spencer. And, further, Simpson also advocates a Postmiocene elevation, which, however, did not result in a connection with Central America.<sup>2</sup>

According to the foregoing, the history of the development of the Central American and West Indian region, as supported by the freshwater Decapods, is the following:

*Central America, the West Indies and the northern margin of South America formed in the Mesozoic period (certainly during Jurassic and Cretaceous) a continental mass (Antillean continent), which was bounded by sea to the north and south. This continent broke up at the end of the Cretaceous, the chief factor in its destruction being the formation of the Caribbean Sea. The northern remnant of this continent, consisting of the Greater Antilles and parts of present Central America, probably remained a unit up to the Eocene. But at the end of the Eocene and during Oligocene and Miocene the connection between the Greater Antilles and the mainland was severed. But it was re-established toward the end of the Tertiary (Pleistocene) and again destroyed in the recent time.<sup>3</sup>*

<sup>1</sup> The subsidence of Cuba at the beginning of the Tertiary, mentioned by Hill (*l. c.*, 1895), refers to the beginning of the Cuban Tertiary—that is to say, to deposits including Eocene and Miocene. See Hill, in *Amer. Journ. Sci.*, Vol. 48, 1894, p. 201.

<sup>2</sup> T. Wayland Vaughan (*Science*, January 24, 1902, p. 148) doubts the Pleistocene connection of Cuba with the mainland, since the recorded finds of Pleistocene Mammals in Cuba are open to discussion, and possibly did not come from this island. But the cases of identical species among the Mollusks, mentioned by Simpson, and the identical species of freshwater crabs discussed here are beyond doubt, and the tendency of the evidence furnished by them is in the same direction as that of the Mammals. We do not believe, however, in a connection of Cuba with North America, but with Central America. (Simpson accepts an Eocene connection with the island of Florida, by way of the Bahamas, which ended in the Miocene.)

<sup>3</sup> This only partly agrees with what we know about the history of Jamaica.

It seems that part of the freshwater Decapods (the identical species) found their way from Central America to the Greater Antilles during the Pleistocene connection, while the genus *Epilobocera* reached the same parts in much older times, in the beginning of the Eocene or even at the end of the Cretaceous. How all these forms were able to get into Central America we shall discuss below.

To which of the two immigrations *Cambarus cubensis* belongs remains doubtful. I am inclined to classify it with the older (Eocene) immigration.

The freshwater crab of the Windward Islands, *Potamocarcinus dentatus*, confirms the view of Simpson that these islands and their fauna have little to do with the Greater Antilles, but rather that they are related to South America. But, while Simpson believes that the (late Tertiary) population of the Lesser Antilles was accomplished by drift, I believe that a land connection is indicated.

#### 7. CONNECTION OF SOUTH AMERICA AND AFRICA.

The presence of freshwater crabs belonging to the family of the *Potamonidae* in the Old World (subfamilies *Potamoninae* and *Deckeniinae*), as well as in the tropical parts of the New World (subfamily *Potamocarcininae*), has led us above (p. 310) to the assumption that there was once a land connection between South America and the West Indies on the one side and Africa on the other. Similar zoogeographical facts have been emphasized chiefly by von Ihering (1891, p. 438, and 1894, p. 406), and, according to him, "all affinities of the freshwater fauna of northern South America direct us to Africa." He believes (we shall discuss this later) that the

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Hill (*Bull. Mus. Harvard*, Vol. 34, 1899) says that at the end of the Cretaceous and the beginning of the Eocene there was an extensive continental period, but that there was a subsidence at the end of the Eocene and in the Oligocene, and then again an uplift at the end of the Oligocene and in the Miocene. The latter is just the opposite movement from what is known for Cuba. It is quite likely that a different fate is to be assumed for the different islands, and it seems that Spencer's idea of contemporaneous subsidence or elevation of the whole region between North and South America is entirely wrong; the orogenetic movements and the changes of level connected with them were, after the first great subsidence of the Caribbean basin, more or less local and affected only limited parts, so that at the same time we may have had opposite movements in different sections of this region.

northern parts of South America (Archiguiana) once formed, during Mesozoic times, a part separated from the rest of South America, which, however, continued eastward across the Atlantic Ocean connecting with Africa. Fernando Noronha and St. Helena are remnants of this land-bridge, which he calls by the name of *Arch-helenis*. This connection was destroyed, according to von Ihering, in the Eocene, or, at any rate, not later than in the Oligocene.

To the numerous instances quoted by von Ihering in support of his theory the distribution of the family of the *Potamonida* adds another one, and the fact that two different subfamilies are found in the Old and the New Worlds, and that the affinities of the American forms with those of Africa and Asia are somewhat obscure, indicates that the connection of both is to be regarded as an old one and that it has been severed long ago. Therefore its existence in Mesozoic times and destruction in the beginning of the Tertiary, as maintained by von Ihering, has much in its favor.

Taking up the geological side of this question, we first have the broad Jurassic connection between Africa and South America assumed by Neumayr (1890). According to this author, and also according to Suess (1888, p. 677 ff.), the whole of the southern Atlantic Ocean did not exist neither during the Jurassic nor during the older Cretaceous (Naumayr, *l. c.*, p. 376), since no traces of deposits belonging to these periods are found in West Africa or on the eastern shores of South America. It was not until the beginning of the Upper Cretaceous that sea washed the eastern parts of Brazil (*l. c.*, p. 389). But the connection of both continents persisted even then, although in a limited degree, and disappeared entirely as late as after the beginning of the Tertiary (*l. c.*, p. 397). Its last remnant (*l. c.*, p. 493) was formed by a chain of islands which extended in the Oligocene from tropical Africa to South America and the West Indies.

This view, however, is not accepted by Koken. In his map (1893, pl. 1) the Cretaceous continents of South America and Africa are absolutely separated in the earlier as well as in the later part of this period, and the Atlantic coast lines of both generally agree with the present ones. In the older Tertiary Koken (pl. 2) draws an island chain (Brazilo-Ethiopian islands) from the West Indies to Africa.

As far as it refers to the Cretaceous period, Koken seems to be mistaken. Although formerly it was supposed that Lower Creta-

ceous deposits are found in West Africa, it was soon recognized<sup>1</sup> that the respective beds are younger, and are certainly not older, than the Middle Cretaceous (in Cameroon); and especially Kossmat (1895) has demonstrated that the Cretaceous beds of West Africa (Angola, Elobi Islands, etc.) belong to the Middle and possibly the Upper Cretaceous (Cenomanian and Lower Senonian), and that they unmistakably possess a South Indian character, being connected probably around the Cape of Good Hope with the Indian Ocean. According to Kossmat, also the Brazilian Upper Cretaceous deposits in Sergipe, Pernambuco, etc.,<sup>2</sup> are of the South Indian type. Farther north, on the coasts of Morocco and Algiers, typical Mediterranean Cretaceous beds are present. The uppermost Cretaceous beds of Angola, however, are said to exhibit traces of the influence of the Mediterranean province (Kossmat, p. 465).

According to these facts we are to form the following idea as to the destruction of the old Brazilo-Ethiopian continent: It existed in its full development during the Jurassic and in the beginning of the Cretaceous time, being the western remnant of the old Paleozoic Gondwana Land, and probably it had the extension assigned to it by Neumayr—that is to say, it connected Africa with the northern as well as with the southern parts (Brazil) of South America. In the middle of the Cretaceous time the southern Atlantic Ocean was formed and the sea extended from the south (connected around the Cape of Good Hope with the Indian Ocean) toward the equator. About the same time, or rather a little later (in the Upper Cretaceous), a branch of the new South Atlantic extended into what is now the valley of the Amazonas river, separating the southern part of the Brazilian mass from the northern (Guiana) (compare below). *But Guiana remained connected with Africa*

<sup>1</sup> See Koenen, A. von, in *Abh. Ges. Wiss. Goettingen*, Ser. 2, Vol. 1, 1897, 1898.

<sup>2</sup> Described by White (*Arch. Mus. Rio Janeiro*, Vol. 7, 1888). Although some of these beds (marine beds in Sergipe and Parahyba) are without any doubt Upper Cretaceous, Branner (*Canadian Meeting Americ. Instit. Min. Engin.*, 1900, p. 17 f., and *Bull. Geol. Soc. America*, Vol. 13, 1902) has lately demonstrated that other marine sediments in Sergipe, Alagoas, Pernambuco, Parahyba, Rio Grande do Norte and Pará belong to the Eocene Tertiary (1902, pp. 47, 64, 85, 91, 96), and also that the freshwater deposits of the Bahia basin are probably Eocene (1900, p. 18).

and this restricted land-bridge going across the middle part of the Atlantic existed probably during the rest of the Cretaceous time and was not destroyed until the beginning of the Tertiary, a chain of islands remaining as late as the Oligocene.

This means, with respect to our freshwater crabs, *that their age goes back at least to the Upper Cretaceous*. During this period the last remnant of the continental connection between Africa and Guiana still existed, and the absence of *Potamonidæ* in South America south of the Amazonas valley further substantiates this assumption, that these crabs did not reach South America prior to the Upper Cretaceous, when the main part of Brazil also took part in this old continental connection. Aside from this fact, we have the consideration that it is not very likely that the age of the fresh-water crabs goes far back in Cretaceous times. Although we have no definite information as to the latter point, we may say, from a morphological standpoint, that the *Potamonidæ* represent a peculiarly specialized side branch of primitive *Cyclometopa*. *Cyclometopa* existed in the beginning of the Cretaceous, but were rare. Thus an Upper Cretaceous age of the *Potamonidæ* is admissible.

The subsequent fate of the *Potamonidæ* in South and Central America, after they immigrated (or originated) in these parts in the later Cretaceous, will be discussed in the next chapter.

#### 8. THE MUTUAL RELATIONS OF NORTH, CENTRAL AND SOUTH AMERICA.

Aside from the peculiarities in the distribution of the freshwater Decapods of America, discussed above, there are several other features which need explanation. They are the following (see pp. 295, 296, 309):

1. The remarkable restriction of the genus *Potamobius* to the western parts of North America, while *Cambarus* is found in the east and south (Mexico).
2. The southern limit of the range of *Cambarus*.
3. The distribution of the *Potamocarcininae* over the West Indies, Central America and the northern parts of South America; their presence in the mountains of Ecuador and Peru and their absence in Brazil south of the Amazonas.
4. The peculiar shape of the areas of *Parastacus* and *Æglea*, which are almost identical, and extend, in the subtropical and tem-



perate parts of South America, from the Pacific to the Atlantic Ocean, but do not extend into the tropical parts.

In order to arrive at an understanding of these points it will be necessary to investigate the history of the origin and the mutual relations of North, Central and South America. It is generally conceded that these three parts have undergone various changes, but as regards the details there is much discussion and erroneous ideas prevail. It will hardly be possible in the following to give satisfactory answers to all of these questions, but we shall endeavor to collect all that is known as relating to the geological history, and we shall thus try to get an idea of the most prominent features of the history of the origin of the Americas.<sup>1</sup>

That America consists of three masses differing tectonically is well known. The nucleus of *North America* is formed by an old northern and eastern mass—the “Canadian shield” and the folded ranges to the south of it. The parts to the west of these were subject to various oscillations during Paleozoic and Mesozoic times, and finally the elevation of the chain of the Rocky Mountains, running in a north-southerly direction, resulted in the present configuration of North America.

*Central America* (including the northern coast of South America) consisted in older times of a system of old ranges with east-westerly strike, forming probably an old Paleozoic and Mesozoic continent (Antillean continent), which was destroyed at the end of the Mesozoic time. Since then Central America and the West Indies are composed only of the remnants of this continent, which in turn have undergone various changes.

*South America* consisted formerly of the old Brazilian plateau, which probably was part of old Gondwana Land (Australia, Africa, South America). The high mountain chains of the Cordilleras in the west did not exist for a long time, and this region was covered by sea probably up to near the end of the Mesozoic time. The elevation of the Cordilleras began at the end of the Cretaceous and continued during the Tertiary.

The present connection of the three Americas did not always

<sup>1</sup> We shall disregard all those questions which are not connected with and illustrated by the distribution of the freshwater Decapods—for instance, the supposed former connection of North and Northeast America with Europe.

exist, and was not brought about until the mutual relations had gone through various and entirely different stages.

a. *North America.*

If we want to get an idea of the configuration of North America during Mesozoic times; we have to consult in the first line Neumayr's well-known map (1890). According to this, in the Jurassic, the northern and eastern parts of North America formed a continental mass, which extended well to the west (Utah peninsula), while the northwest was covered by the sea that separated America from Northeastern Asia. At the same time this continent (Nearctic) was bounded by sea to the south, Mexico and the West Indies being submerged.<sup>1</sup> This representation, however, needs correction, chiefly as regards the West Indies, as we have seen above.

Differing but little from the view taken by Neumayr is that of Koken (1893, pl. 1) with respect to the Lower Cretaceous period; but here the land extends considerably to the northwest and includes parts of Mexico, a conception which is also to be modified, as we shall presently see.

The general history of North America during the Cretaceous period is best represented by Dana (1895, pp. 813, 874, 881). According to him, Western North America was largely land during the Lower Cretaceous and continuous with the rest. In the Upper Cretaceous, however, chiefly in its earlier part, a central depression became evident, which extended from the south (Gulf of Mexico) northward and possibly reached the Arctic Ocean, dividing the continent into an eastern and a western half. The western half, as we have seen above (p. 318), became connected across Bering Sea with Asia at about this time.<sup>2</sup> At the end of the Cretaceous (Laramie) and in the beginning of the Tertiary an extended elevation began, which culminated in the formation of the Rocky Mountains, and by this process the interior Cretaceous sea became land again, which resulted in the reconnection of Western and Eastern North America. But, although there was a geographical union, Eastern and Western North America remained separated bionomi-

<sup>1</sup> Compare, also, Logan, W. N., in *Journ. of Geology*, Vol. 8, 1900, but here the Jurassic ocean of the Northwest is considerably reduced in size and represented only by a shallow bay.

<sup>2</sup> Temporarily the Cretaceous sea of the interior was connected in British Columbia with the Pacific (see Kossmat, 1895, p. 474).

cally, the Upper Cretaceous sea barrier being replaced by a barrier formed by the Rocky Mountains.<sup>1</sup>

Looking now toward Mexico and its continuation southward, we shall refer in the first place to the papers of Hill (1893 and 1898). The history of Mexico in Pre-Cretaceous times is very obscure. Possibly it was covered by sea, as is also assumed by Neumayr, in the Jurassic, at least in part (Hill, 1898). But it seems to be well established that in the Lower Cretaceous (Hill, 1893) almost all of Mexico was submerged from the Atlantic to the Pacific side. This Lower Cretaceous sea was limited on the north by the southern coast of the North American continent, which extended from the old Appalachian region across the present Indian Territory and New Mexico to the Mexican province of Sonora.<sup>2</sup>

In the middle of the Cretaceous period (at the end of the Comanche series, Gault) a large part of Mexico became land, forming a southern continuation of the western part of North America, which was separated in the Upper Cretaceous from the eastern, and which therefore extended from British Columbia<sup>3</sup> to the Isthmus of Tehuantepec. This strip of land formed during this period a very important barrier, separating the marine faunas of the Pacific and Atlantic Oceans. While both faunas were more or less connected during the Lower Cretaceous across Mexico, they became separated later and never again communicated in this region.

The Isthmus of Tehuantepec consists, according to Spencer,<sup>4</sup> of the identical Lower Cretaceous deposits found in Mexico, and, further, according to Sapper,<sup>5</sup> Cretaceous rocks are found in the

<sup>1</sup> This barrier was probably emphasized by the development of desert conditions in and at the foot of this mountain range. Compare Scott, W. B., *An Introduction to Geology*, 1897, p. 500: "Probably the upheavals at the end of the Bridger and at the end of the Eocene had made the climate much drier by cutting off the moisture-laden winds."

<sup>2</sup> In 1898 (pp. 243 and 259) Hill qualifies his views, and says that it is doubtful whether the whole country (Mexico) was entirely submerged at any one time during this period. He thinks it was a mere shifting of the barrier between the Atlantic and Pacific. Compare, also, Stanton, T. W., in *Journ. of Geology*, Vol. 3, 1895, p. 861.

<sup>3</sup> And these parts must have been connected, as we have seen above, with Northeastern Asia.

<sup>4</sup> *Bull. Geolog. Soc. America*, Vol. 9, 1897.

<sup>5</sup> *Boll. Instit. Geol., Mexico*, Vol. 3, 1896.

Mexican State of Chiapas, which adjoins Guatemala. As regards Guatemala, we know that here old rocks appear which belong to the system of the Antillean continent (see above, p. 342). Thus we have reason to assume that, while Mexico was covered by the Lower Cretaceous seas which separated North and Central America, this whole region became land at about the middle of the Cretaceous, thus effecting a connection of Western North America with Central America (Guatemala) or with the old Antillean continent. This seems to be also the view of Hill, and he likewise believes that this connection was never subsequently interrupted.<sup>1</sup>

The result of the foregoing discussion is that during the Jurassic, and especially during the Lower Cretaceous, North America formed a unit, which was separated from Asia and which was also circumscribed by a shore line in the south, being disconnected from Central America. In the middle part of the Cretaceous Mexico was elevated, and this new-formed land connected the western part of North America with the Antillean continent. At about the same time a connection of Western North America with Northeastern Asia was established (by way of Bering Sea), and the Mexican Gulf extended northward, separating Western from Eastern North America.

*Thus we have, in the Upper Cretaceous, a strip of land extending from Northeastern Asia over Bering Sea and over the western side of North America to Mexico and the Antillean continent. Eastern North America was separated from this strip.*

*In the beginning of the Tertiary Eastern North America became reunited to this western section.*

*At the end of the Tertiary the Beringian connection with Asia was interrupted (see above, p. 317).*

This would lead us for our Crustaceans to the following conclusions: We have seen above (p. 319) that at any time, beginning in the Upper Cretaceous, *Potamobius* may have invaded the western parts of North America. This is again supported by the preceding

<sup>1</sup> See Hill, 1893, p. 323. Spencer (1897) assumes that there was a reestablishment of the connection of the Atlantic and Pacific Oceans across the Isthmus of Tehuantepec in late Tertiary times. The evidence for it, however, is entirely insufficient. The gravels found on the passes of the isthmus are of no value, since their marine character has not been demonstrated. Compare, also, Hill, 1898, p. 262, footnote.

considerations, in so far as it is confirmed that *Potamobius* cannot have been present in North America during the Lower Cretaceous, otherwise the remarkable restriction to the west would be inexplicable. But the genus must have immigrated during the Upper Cretaceous, since fossil remains of *Potamobiidae*<sup>1</sup> are known from the Eocene of North America. This latter fact, therefore, narrows down the time of immigration to more definite limits (those of the Upper Cretaceous), and at the same time explains its restriction to the west. During this period the western parts of the country were separated from the eastern by sea. At the same time there was a possibility for the crayfishes to reach Mexico, and it is easily understood that *Potamobius* then sent a branch southward, which subsequently developed on the Mexican plateau into *Cambarus*. After this, in the beginning of the Tertiary, *Cambarus* had a chance to migrate by way of Texas into Eastern North America, where it reaches its culmination in the present time.

The morphological differentiation of *Cambarus* from *Potamobius* probably took place in the beginning of the Tertiary, after the ranges of these genera had become separated. This separation is apparently due to a climatic change in the region between Mexico and central California, where desert conditions developed. This desert climate is not so pronounced on the eastern side of the continent, near the Atlantic coast in Texas, and, consequently, the area of *Cambarus* is not here interrupted between Mexico and the United States. A subsequent connection of the ranges of *Potamobius* and *Cambarus* in the interior of North America (in the region of the Rocky Mountains and the plains adjacent to their eastern slope) was impossible on account of the topographic and climatic barrier existing there in Tertiary times, which has been mentioned above (p. 354). The Rocky Mountains themselves and the arid regions are not favorable for the freshwater crayfishes. Thus the areas of both genera remained separated, and only in one case a species (*P. gambeli*) has crossed the continental divide in the region of the Yellowstone National Park. This, however, is very likely due to the capturing of streams that originally belonged to the Pacific slope by the Yellowstone river.

*b. Central America.*

The tectonic unity of the old Archaic and Paleozoic rocks known

<sup>1</sup> *Cambarus primævus* of Packard, from the Eocene of Western Wyoming, which is, however, according to Faxon (1885, p. 155), rather a *Potamobius*.

from Guatemala to Venezuela is also emphasized by Hill (1898, p. 239 ff.), and he also thinks that, during Mesozoic times, a continuous continental mass may have existed here, which reached as far as Trinidad. We have seen above that the destruction of this continent was probably due, in the first place, to the formation of the Caribbean depression, at the end of the Cretaceous. This also agrees with Hill's view (1898, p. 260 f.) that during the whole of the Cretaceous, or at least during the larger part of it, the Atlantic and the Pacific Oceans were separated in the region of Central America—that is to say, that there was a land connection between the northern parts of Central America and northern South America. But, according to Hill, this connection is not identical with the present isthmian region, but was situated chiefly to the west of it.

We have nothing to say against a western extension of this Cretaceous land (which probably extended as far as the Galapagos Islands), but we believe that the isthmian region and the present Caribbean Sea also were land during this time; the main point is, that there was a connection between Guatemala, Honduras, Nicaragua, and the Greater Antilles on the one side, and northern Venezuela on the other.

These conditions changed considerably during the Tertiary. First, the Caribbean Sea was formed, and possibly it extended farther to the west and southwest than it does now. At least, parts of the present land-bridge, the Isthmus of Panama, were covered entirely by sea in the earlier Tertiary, and that this sea reached from the present Caribbean Sea across to the Pacific is beyond doubt. In the first line, the part through which the Panama canal is to be built is composed entirely of deposits that are not older than Eocene and Oligocene (Hill, 1898, p. 236), and this well agrees with the investigations of Douvillé,<sup>1</sup> and Bertrand and Zurcher:<sup>2</sup> the Old Tertiary sea (Eocene and Oligocene) must have here extended entirely across the isthmus, from the Atlantic to the Pacific.

The same seems to be true for the Nicaragua canal. According to Hayes,<sup>3</sup> there are no rocks along this route that are older than Tertiary, and the Tertiary deposits probably belong to the Eocene and Oligocene. The remarkable discovery has been made that

<sup>1</sup> *C. R. Soc. geolog. France*, 1898.

<sup>2</sup> Bertrand, M. et Zurcher, O. *Etude géologique sur l'Isthme de Panama*, 1899.

<sup>3</sup> Hayes, C. W., "Physiography and Geology of Region Adjacent to the Nicaragua Canal Route" (*Bull. Geol. Soc. America*, Vol. 10, 1899).

sediments on the Pacific side contain the same fossils as the corresponding ones on the Caribbean side, which is an important addition to Hill's observations.

Between these depressions of the isthmian region, filled out by older Tertiary deposits, there are Archaic rocks at various places; we know of such not only from Guatemala and Honduras, but also from northern Nicaragua (Hayes), Costa Rica (Hill, Hayes), and even farther east, beyond the Panama canal, in the Cordilleras of San Blas. Thus it seems that the present isthmus, from Nicaragua to Colombia, consisted during the older Tertiary of a series of islands separated by ocean straits.

According to the unanimous opinion of Hill, Hayes, Bertrand and Zucher and others, these straits (Nicaragua and Panama) became dry in the Middle Tertiary, *i. e.*, in the *Miocene*, and, consequently, the connection of North and South America was then established.

Although this Eocene and Oligocene communication of the oceans is admitted by Hill, he is inclined to minimize its importance. Moreover, he assumes (1898, p. 263) that to the southward and westward, toward the Pacific, a large land mass must have existed, from which the material of the marine deposits of the isthmus was derived, and, further, he believes that this land mass chiefly extended in a north-southerly direction, probably connecting North and South America. I think we do not need this land, and even if we accept its existence,<sup>1</sup> it hardly formed, in the earlier Tertiary, a connection of the Americas. Be that as it may, the insular elevations of the isthmus, and the masses of old rocks to the north of it, in Nicaragua, Guatemala, Honduras, and in the supposed connecting land with Jamaica and Cuba (see above, p. 347), were in our opinion sufficient to furnish material for those Old Tertiary sediments in the isthmian region.<sup>2</sup> On the other hand, any

<sup>1</sup> Since we need, as I most emphatically believe, a connection with Galapagos Islands; this subject, however, is outside of the present question.

<sup>2</sup> Hill himself (1898, p. 263) discusses the idea that the land to the north of the isthmus may have furnished the material, but dismisses it, since here "we are confronted by great depths." Now, in my opinion, great depths are no fundamental objection, and just in this case the character of the sea bottom in the region between Honduras, Jamaica, Cuba and Hayti indicates that important disturbances have occurred here, and, in the first place, the deep submarine rift valley, known as "Bartlett deep," may be of a very recent age.

land mass to the south and west of the isthmus cannot have formed an Old Tertiary barrier completely separating both oceans, since we need an interoceanic communication during this time, as we shall presently see.

Our opinion is, that during the Cretaceous there was a connection between northern Central America and northern South America, the Antillean continent still being more or less intact. At the beginning of the Tertiary, however, and after the formation of the Caribbean Sea, an oceanic connection existed between the Atlantic and Pacific in the isthmian region, and this communication existed up to the Miocene, separating North and South America. But afterward, beginning in the Miocene, the isthmus was elevated, reconnecting the separated chief remnants of the Antillean continent, and at the same time North and South America. The Atlantic and Pacific Oceans were separated, and never again communicated, either here or elsewhere.

We here arrive at a result which differs considerably from von Ihering's ideas as to the relations of North and South America: von Ihering believes (1894, p. 405) that both continents were separated by Cretaceous sea, and that Central America was entirely submerged at this time; the origin of the Isthmian land-bridge is also placed by von Ihering in the Miocene.

For our Crustaceans, we are to draw from this the following conclusions:

The presence of *Potamocarcinina* in the present continental parts of the old Antillean continent, in Nicaragua, Guatemala (to which we must add the southern parts of Mexico), the isthmian region and Venezuela, is due to the Cretaceous connection of these parts; the presence of the genus *Epilobocera* in the Greater Antilles is due to the former connection of these islands with the mainland, and belongs to the same land period, or to the continuation of it in the earlier part of the Tertiary. After the separation of the Greater

<sup>1</sup> This idea well agrees with the character of the present Atlantic and Pacific marine littoral faunas in the Central American region. These faunistic facts are often incorrectly represented and understood, and Hill's argument against the importance of the interoceanic communication in older Tertiary times is based upon such a misunderstanding. I have studied this question chiefly with reference to the marine Decapod Crustaceans, and shall give below a correct representation of the actual conditions of the faunal relations of both oceans. See Appendix.



Antilles from the mainland, there was left on these islands an isolated stock of primitive freshwater crabs, now known under the name of *Epilobocera*. On the mainland, these primitive forms disappeared, or changed into what is now known as the genus *Potamocarcinus*, and although in the beginning of the Tertiary the continental range of this genus was much cut up, chiefly in the region of the isthmus, the different parts were reunited in the Miocene, forming a unit that extended from northern Central America to Trinidad and Guiana. This explains the uniform distribution of *Potamocarcinus* over this region. In the later Tertiary we had a second union of the Greater Antilles with northern Central America, which explains the immigration of identical species of *Potamocarcinus* from Mexico into Cuba and Hayti. The Lesser Antilles were probably connected in the later Tertiary with Venezuela, and a species of freshwater crabs reached them by this way.

*c. Relation of Venezuela to the rest of South America. The Orinoco Valley.*

The northern coast range of Venezuela belongs, as has been stated, to Central America. To the south, on the slope toward the Orinoco, it is fringed by extensively developed Cretaceous deposits, which are also known from Trinidad in a similar position. These deposits are said to belong to the Lower Cretaceous (Suess, 1885, p. 688), and to extend westward far into Colombia. To the south of this zone, in Venezuela, there are (Suess, *ibid.*) younger Tertiary marine beds, which, in part, enter this region through a depression extending southward from the Bay of Barcelona on the northern coast of Venezuela.

This would indicate that during the Lower Cretaceous, the old Antillean continent was bounded on the south by sea (see above, p. 343), which separated it from the old granitic masses of Guiana. The apparent lack of Upper Cretaceous deposits, with the exception of a small region of western Venezuela, points to the assumption that at the end of the Mesozoic time (Upper Cretaceous) both regions were connected. Then again, in the later Tertiary, they were separated, at least in part, by sea that entered into the Orinoco valley (Suess, 1888, p. 161).

The Lower Cretaceous sea not only separated Venezuela and Guiana, but apparently continued westward, into Colombia, Ecuador and Peru. Indeed, there are in the western chain of the

Cordilleras in Peru and Bolivia many exposures of old (Archaic and Paleozoic) rocks; but the fact that in this region (from Colombia to Bolivia) Lower Cretaceous of the Mediterranean type has been discovered right in the Cordilleras,<sup>1</sup> renders it possible that those older rocks were originally covered by Mesozoic deposits, which were removed subsequently by erosion; and this is also the view of Suess (1885, p. 684, and 1888, p. 683), since he takes it for granted that the Cretaceous beds of the Upper Amazonas (and Orinoco) valley once continued across the whole continent to the Pacific Ocean.

Thus there would result, in Lower Cretaceous times, a complete separation of Central from South America by a sea, which extended from the region of the mouth of the Orinoco westward to Ecuador and Peru, *connecting the Atlantic and Pacific Oceans: in the Upper Cretaceous, however, Guiana was united with Venezuela.*

The *Potamocarcinina*, which, as we have seen above (p. 351), arrived in Guiana in the Upper Cretaceous (by way of the connection with Africa), found at this same time a land connection with the northern parts of Venezuela, and generally with the Antillean continent, and this explains their general distribution over Central America and the West Indian region, as set forth above (p. 308), and the origin of this distribution consequently falls in the *Upper* Cretaceous.

#### *d. South America.*

The separation and isolation of South America from Central, resp. North America during Mesozoic times as well as in the beginning of the Tertiary, forms the fundamental idea of von Ihering's Archiplata and Archhelenis theory (1891). But, according to him, the line of separation was situated in the present Amazonas valley, and existed during the Jurassic, Cretaceous and the Eocene; in the Oligocene the elevation of the Cordilleras began, and Archiplata (the southern part) was united with Archiguiana (Guiana and Venezuela), and it was not until the beginning of the second half of the Tertiary (Miocene) that these latter parts became united with North America by the formation of the Isthmus of Panama.

We can accept this view only in part, since the very important

<sup>1</sup> Hyatt, A., in *Proc. Boston Soc. Nat. Hist.*, Vol. 17, 1875, p. 365 ff.; Steimann, in *N. Jahrb. Mineral., etc.*, 1881, 2 p. 130 ff., 1882, 1 p. 166 ff., and Gerhardt, *ibid.*, Beil., Bd. 11, 1897.

interoceanic connection through the Orinoco valley, discussed above, is not taken account of, and since, as we shall see presently, the relations between Guiana and Brazil and between Guiana and Venezuela are much more complex than v. Ihering assumes.

Considering the tectonic configuration of South America, we are to mention, in the first place, that the whole eastern part is formed by the so-called *Brazilian mass* (Suess, 1885, p. 655 ff.): this is an old Archaic-Paleozoic plateau, which was possibly connected, from very early times up to the Lower Cretaceous (see p. 350), with Africa. Part of this mass is formed by the mountains of Guiana (Suess, 1885, p. 658), and the present valley of the Amazonas is a symmetrical syncline within the old plateau, in the centre of which are Carboniferous beds and, on top of the latter, Upper Cretaceous deposits. Thus the Amazonas valley was apparently land during most of the Mesozoic time, and Guiana was connected with Brazil; but in the Upper Cretaceous it was a wide sea, the northern and southern shores of which were formed by Paleozoic rocks (Suess, 1885, p. 660). This sea extended from the Atlantic westward into the region of the Upper Maranhão, in the Cordilleras, and probably connected with the Pacific Ocean (Suess, 1888, p. 683), which is very likely, since the western shore of the old Brazilian mass hardly extended to the eastern foothills of the Cordilleras (in a certain region, the present river Madeira marks the western boundary), and since it is quite sure that the Cordilleras were sea during the Jurassic as well as the larger part of the Cretaceous. This results in an Upper Cretaceous interoceanic connection between the southern Atlantic and the Pacific, which was situated about where the Amazonas valley now is. *This Upper Cretaceous strait agrees with the sea that separated von Ihering's Archiplata and Archiguiana*, but it is well to emphasize the fact that it is restricted, as a separating strait, to the *Upper Cretaceous* period: during previous times, especially the Jurassic and Lower Cretaceous, it did not exist at all, and later it was changed into a bay, as we shall see below. The interoceanic connection during the earlier Cretaceous was not situated here, but went by way of the Orinoco valley (see above, p. 360). The directions of both straits converge to the westward, and it is possible that they actually met, if they coëxisted at any time: but generally, we are to maintain *that the separation of Central and South America during the Lower Cretaceous was effected by the Orinoco Strait, and that at this time Guiana was*

*united with Brazil, to which it belongs tectonically, while, in the Upper Cretaceous, Guiana was united with Central America, and was separated from Brazil by the transgression of the Atlantic Ocean in the Amazonas valley.*

This latter strait thus formed a continuation of the South Atlantic Ocean, which came into existence, as we have seen above (p. 350), at about the middle of the Cretaceous.

The Upper Cretaceous conditions were generally preserved in this region during the beginning of the Tertiary, and the Eocene and Oligocene sea extended, in the Amazonas transgression, far to the west (brackish Oligocene deposits are known near Pebas, Peru). But during this time (older Tertiary), the elevation of the Cordilleras must have become evident<sup>1</sup> in the western parts of this interoceanic connection, since older Tertiary deposits are wanting in this region. Thus those parts which now comprise Colombia, Ecuador, Peru and Bolivia became land, and the Amazonas Strait was shut off from the Pacific Ocean, being transformed into a deep bay, which occupied the Amazonas valley as far as the foothills of this new elevation (Cordilleras). Therefore, this interoceanic connection was interrupted in the beginning of the Tertiary, the main part of South America, or the old "Archiplata" of von Ihering, becoming united with northern South America (Venezuela and Guiana). But we have seen above (p. 344) that at the same time (earlier Tertiary or uppermost Cretaceous) another interoceanic connection had formed in the isthmian region, and this replaced the Amazonas connection of the Upper Cretaceous era.

The old connection of the Brazilian mass with Africa continued in part as we have seen (p. 350) during the Upper Cretaceous, for its northern portion, Guiana. That is to say, an intermigration of the faunas of Guiana and Africa was yet possible in the Upper Cretaceous. The fact that during this time (and in the beginning of the Tertiary) a strait or bay extended along the region of the Amazonas river as far as the Pacific Ocean (or as far as the Cordilleras), furnishes the explanation for the zoogeographical fact that animals immigrating from Africa into Guiana during the Upper Cretaceous could reach Central America and the West Indies, but not those parts of Brazil which are to the south of this old Amazonas Strait: this seems to apply to our *Potamonida*, and

<sup>1</sup> The first signs of an elevation belong to the Upper Cretaceous.

explains their general absence south of the Amazonas. The extension of the range of these freshwater crabs into Colombia, Ecuador and Peru was not obstructed during the older Tertiary, since during this time these parts became land and were connected with Venezuela.

Regarding the extension of the old Brazilian mass (Archiplata) to the south, we know that the old Archaic, Paleozoic and Old-Mesozoic rocks continue in southern Bolivia and northern Argentina, into the eastern Cordilleras (Suess, 1885, p. 661); in Argentina, these rocks prevail in the northern parts: they are also found in the Pampean Sierras,<sup>1</sup> but do not seem to extend southward beyond the province of Buenos Ayres (Suess, 1885, p. 664). To the south of these parts the whole of Patagonia was apparently covered by the Cretaceous sea (Suess, 1888, p. 683, and above, p. 338). The Brazilian continent was also surrounded in the west by Jurassic and Cretaceous sea, as is demonstrated by the presence of the respective deposits in the region of the Chilian-Argentinian Cordilleras (see p. 338). As we have seen above (*ibid.*), it is very probable that during the Jurassic and a larger part of the Cretaceous era, the Brazilian mass was separated by this sea, which occupied present Patagonia and the site of the Cordilleras, from another continental mass lying to the west, southwest and south of it, which was formed by the present Chilian coast range and its southern continuation, which belonged, at least during the Cretaceous, to the Antarctic continent. At the end of the Cretaceous a land period began in these regions which culminated in the Eocene, and which effected a connection of the old Antarctica with Archiplata, chiefly in the region of the Chilian-Argentinian Cordilleras. This connection made possible the immigration of *Parastacus* into the southern parts of Archiplata (Argentina, Uruguay, southern Brazil), and it has remained up to the present time, although parts of Patagonia were again submerged during the course of the Tertiary.

The results obtained in the foregoing concerning the history of the American continent may be summed up as follows.

1. America originally consists of *three parts*: *North America* (its nucleus being in the East), the *Antillean continent* (comprising the West Indies, Central America and the northern coast of Venezuela) and the old *Brazilian mass* (Archiplata). Also a *fourth part* enters

<sup>1</sup> Valentin, J., *Bosquejo geologico de la Argentina*, 1898.

the present boundaries of South America, which is formed by the *Chilian-Fuegian coast range*, once a *part of Antarctica*.

2. *North America* was separated during the *Lower Cretaceous* from Central America. During the *Upper Cretaceous* it was divided into an eastern and a western portion; the western was definitively connected at this time with Central America. In the beginning of the *Tertiary* the eastern portion was reunited with the western, and thus the whole of North America, from the Arctic Ocean to the Gulf of Mexico and the Caribbean Sea, became a unit.

3. *Central America* existed as a continental mass up to the end of the *Cretaceous*. Being originally separated from North America, it became united with it in the *Upper Cretaceous*. By the formation of the Caribbean Sea it was broken up and consisted, in the *beginning of the Tertiary*, of two main parts: a *northern*, belonging to North America, and a *southern*, which became united with South America, then undergoing the process of construction. Both parts were separated by the Old Tertiary interoceanic connections at Panama and Nicaragua.

The *southern part* of Central America was originally (Lower Cretaceous) bounded on the south by sea, which occupied the region from the Orinoco valley westward. In the *Upper Cretaceous* Guiana was connected with Venezuela, and thus Central America was connected also with Africa. To the south of these parts was the Upper Cretaceous interoceanic connection of the Amazonas valley. In the *beginning of the Tertiary*, what was left of Central America in the south (Venezuela and Guiana) was united with the Brazilian mass by the beginning of the upheaval of the Cordilleras, by which parts of Colombia, Ecuador and Peru became land.

In the *middle of the Tertiary* (Miocene) the interoceanic connection in the isthmian region became land, and thus North America and the northern remnants of Central America were united with the southern remnants of Central America and South America.

4. *South America* consisted in the beginning (Jurassic and Lower Cretaceous) of the Brazilian mass (Archiplata), which included Guiana, and a smaller part which is perhaps of Cretaceous age, represented now by the Chilian coast range. Archiplata was connected with Africa up to the middle of the Cretaceous. In the *Upper Cretaceous*, Guiana was separated from Brazil by the interoceanic connection of the Amazonas valley and Archiplata became an island. At the *end of the Cretaceous*, and chiefly during the

*Eocene*, Archiplata became united with the Chilian coast range by the elevation of the Cordilleras, and it was thus connected with Antarctica. And, further, in the *beginning of the Tertiary*, Archiplata connected, by way of Peru and Ecuador, with Central America. This resulted in the final formation of South America (in its rough outlines) which, however, was still in communication with Antarctica. Finally, in the *middle of the Tertiary*, South America was united with North America (in the isthmian region) and was severed from Antarctica, and this represents the chief features of the present conditions.

We have seen that during the geological development of the Americas *interoceanic connections*, which were directed east-westerly, and united the waters of the Atlantic and Pacific Oceans, have repeatedly played a part. These connections being extremely important for marine zoogeography, have often been referred to by various authors, but have generally been misunderstood, the value of a determination of the exact time of their existence being neglected. So it will be worth while here to put them together by themselves.

*Interoceanic connections of the Atlantic and Pacific Oceans.*

1. In the *Lower Cretaceous* there were *two* connections: *a. across Mexico*, and *b. through the Orinoco valley*. Both probably united the marine fauna of the Mediterranean province with that of the (Indo-) Pacific.

2. In the *Upper Cretaceous* we have the connection through the *Amazonas valley*. This united the South Atlantic fauna, which, in this period, formed part of the Indo-Pacific, with the identical fauna of the eastern Pacific.

3. In the *Older Tertiary* there existed the *Panamic connection*, which united the fauna of the Atlantic, the chief element of which is Mediterranean, with that of the Indo-Pacific.

4. In the *Later Tertiary* no interoceanic connection existed, the Atlantic and Pacific faunas being sharply separated. These conditions continued up to the present time.

It is impossible to say at present whether there were any transitions between these different stages. A coëxistence and union of the connections 1 and 2, at about the beginning of the Upper Cretaceous, is possible in the region of the Upper Orinoco and Upper

Amazonas. But we have no evidence for this, the Geology of the respective countries being too incompletely known.

#### 9. THE RELATIONS OF AFRICA TO THE REST OF THE WORLD.

We have seen (p. 303) that for the two main divisions of the range of the *Potamoninae* in the Old World Egypt and the Nile valley form an actual connection; but examining this more closely we find that this subfamily cannot have migrated along this route from Africa to India (or vice versa), but entered Egypt from two opposite directions, from the south (Central Africa) and the north (resp. northeast) over Persia, Mesopotamia and Syria.

The causes why this way was not open in former times have been briefly mentioned above (p. 333), and we shall here try to investigate the relations of Africa and Asia with respect chiefly to this northern connection. For this purpose we are to discuss also the northern boundaries of Africa with reference to Europe. This is the more important, since we have to consider the alleged fact that fossil forms of the *Potamoninae* have been found in Miocene fresh-water deposits of Oeningen (Switzerland), Sigmaringen (Southern Germany) and Northern Italy.<sup>1</sup>

Very important for a study of these questions is the former existence of a *Central Mediterranean Sea*, as Neumayr calls it (1890, pp. 332, 333, and map p. 336), or the *Tethys* of Suess (1894). This ancient sea goes back to Paleozoic times and covered in Mesozoic times the whole of Middle and Southern Europe, the present Mediterranean Sea, Northern Africa and extended eastward over Asia Minor, Syria, the Caucasus Mountains and Mesopotamia as far as Northern India. In the east a large bay extended southward along the East African coast, which separated the Indo-Madagassian peninsula (Lemuria) from Africa. In a westerly direction the Tethys was broadly connected with the Atlantic Ocean, leaving only the island of Spain (Meseta) uncovered.

In these general outlines the Tethys existed in Jurassic as well as in Cretaceous times, thus completely circumscribing the African continent toward the north and northeast. Europe did not then exist at all as a continental mass and Africa was separated from the Sinic continent by an eastern continuation of the Tethys, the

<sup>1</sup> *Thelphusa speciosa* Mey. and *Th. quenstedti* Zitt., see Zittel, *Handbuch d. Paläontol.*, Vol. 2, 1885, p. 714. These forms have a remote resemblance to the subgenus *Potamonautes*, if they belong here at all.



*Strait of Bengal.*<sup>1</sup> The only connection of Africa during these times was with South America, the old Archiplata (Jurassic and Lower Cretaceous) and the old Archiguiana (Archhelenis, Upper Cretaceous). On the southern margin of the Tethys, as sketched above, there is a zone in the desert region of North Africa and Arabia, where Jurassic deposits are wanting and Cretaceous directly overlies Paleozoic beds. This indicates a farther extension of Africa northward in Jurassic times and a transgression of the sea southward in the Cretaceous (Neumayr, 1890, p. 386). The deposits of the Cretaceous sea can be traced very distinctly in a broad belt from Syria over Arabia, Persia, Afghanistan and Beluchistan to Northern India.

Also in the Older Tertiary (Neumayr, p. 480) the Central Mediterranean Sea reaches from the Atlantic Ocean to India, and it was not until after the end of the Oligocene that its unity was destroyed. In the beginning of the Miocene Western Asia became largely land, and thus a broad connection was established from Asia to Africa (India to Arabia), and at the same time from Asia to Europe, which was then forming (Neumayr, 1890, p. 501 f.).

In detail the processes in the northeastern part of Africa were the following: Arabia during Mesozoic and the greater part of Tertiary times was broadly connected with Africa. The Red Sea did not exist, according to the unanimous opinion of all writers (Neumayr, Suess, Gregory, Blankenhorn and others). The origin of the Red Sea falls late in Tertiary times, after the connection of Africa with India was long established, and thus, in the second half of the Tertiary, a regular exchange of the faunas of Africa and India could take place, for which we possess ample evidence.

The Red Sea is a rift valley, which is tectonically connected with the valley of the Jordan river in Palestine.<sup>2</sup> The most detailed investigations on this question have been published by Blankenhorn.<sup>3</sup> According to this author, the Mediterranean Sea (the western part of the old Tethys) in Miocene times sent a wide bay to the southeast, which extended as far as the southern end of the Gulf of Suez, which, of course, did not then exist, and the Nile

<sup>1</sup> Which, however, was temporarily interrupted during the Upper Cretaceous. See above, p. 330.

<sup>2</sup> See Gregory, J. W., in *Proc. Zool. Soc. London*, 1894, p. 165.

<sup>3</sup> Blankenhorn, M., in *Centralbl. f. Mineral.*, etc., 1900, p. 209 ff.

valley.<sup>1</sup> The latter and the Red Sea originated in the Pliocene. Into the Nile valley entered the Pliocene Mediterranean Sea. It then changed into a series of inland lakes, and finally, in the middle Diluvial time, it became a river valley. The depression of the Red Sea was occupied first (Pliocene) by inland lakes, and finally, toward the end of the Pliocene, by the Indian Ocean, which entered it from the south.<sup>2</sup> The present separation of Africa and Arabia (Asia), which is nearly complete, belongs, therefore, to a very recent date. In the later Tertiary Southern Asia and Africa were not distinguished zoogeographically, while in older times (Pre-Miocene) there was a complete separation of Africa (including Arabia) from the Sinic continent, and only during the second half of the Cretaceous was there a limited connection by way of Madagascar and the Indian peninsula.<sup>3</sup>

The old isolation of Africa was ended not only in these eastern parts during the Tertiary, but also in the northwest changes occurred which extended Africa and brought it into contact with Western Europe.

The Cretaceous sea covering Northwestern Africa was no doubt considerably reduced in the Tertiary. Indeed, there are Tertiary deposits in this region, and according to Suess (1888, p. 155), the Middle Tertiary sea probably also covered the Western Sahara. But about this time apparently a land connection was formed to the north toward the old Spanish Meseta. According to Bergeron,<sup>4</sup> the Algerian Sahara possesses deposits from the Senonian to the Pliocene, but these are bounded in the west by a Cretaceous mountain

<sup>1</sup> In the region of the Nile valley there was a river, but this was not the Nile, but came from the west out of the Libyan desert.

<sup>2</sup> An actual connection of the Red Sea and the Mediterranean Sea is very doubtful, but was possibly established for a short time in the beginning of Diluvial times, when the Mediterranean Sea became cold. The improbability of a connection of both seas is especially emphasized by Jousseume (*Ann. Sci. Nat.*, Ser. 7, Vol. 12, 1891). According to him, the Red Sea is Quarternary (Diluvial).

<sup>3</sup> The oceanic connection from the Gulf of Aden across the Sahara desert to the Atlantic (Senegambia), advanced by Jousseume (*l. c.*), has no geological support. It is founded upon an alleged similarity of the Mollusk faunas of both parts, which, however, needs closer investigation and might possibly find its explanation in the configuration of the Pre-Miocene Tethys, which reached from the Persian Gulf to the Mediterranean Sea and Atlantic Ocean.

<sup>4</sup> In *Mem. Soc. Ingen. civ. France*, 1897.

range running north-south. In Algeria we have, according to Lap-  
parent,<sup>1</sup> deposits of Cretaceous and Eocene age, but only traces of  
Oligocene, and thus we can place the upheaval of these parts at the  
end of the Eocene, and probably at this time the connection with  
Southwestern Europe began to develop. The mountain range  
along the northern coast of Algiers, as far as the Strait of Gibraltar,  
consists of rocks which (see Suess, 1883, p. 293 ff.) are also found  
in the so-called Betic Cordilleras (*ibid.*, p. 298) in Southern Spain,  
and the tectonic unity of these ranges of Algiers and Spain is  
especially emphasized by Suess, as well as their tectonic connection  
with the Apennines and the Alps. The origin of all these moun-  
tain chains was near the end of the first half of the Tertiary, about  
the Oligocene time.

But this connection of the northwestern parts of Africa and of  
Southern Spain with the rest of Africa did not constitute a com-  
plete union with Europe. We know that the central and northern  
region of Spain, the Iberian Meseta, is an old land, but that to the  
south and north of it, on the one side along the valley of the  
Guadalquivir river in Spain, on the other in the region of the  
Garonne river in France, connections of the Mediterranean Sea with  
the Atlantic Ocean existed. According to Suess (1885, p. 381; see  
also Neumayr, 1890, p. 516), in the valley of the Guadalquivir  
there are Tertiary deposits, reaching from the Atlantic to the Medi-  
terranean Sea, which belong to the first and second Mediterranean  
stage—that is to say, to the Miocene—while deposits of the third  
Mediterranean stage (Pliocene) have not been found. Conse-  
quently this strait (Betic Strait) became dry at the end of the  
Miocene, and by this process the northern part of Spain was united  
with the southern and with Algiers and Africa.

The disappearance of this strait was the last step which resulted  
in a definitive connection of Africa with Europe, since the strait in  
the region of the Garonne river, in Southern France, became prob-  
ably land a little earlier, namely, at the end of the Oligocene (see  
Suess, 1885, p. 382 ff., and Neumayr, 1890, p. 516).

But it is to be borne in mind that possibly the conditions were  
not so simple as has been represented above. According to Lap-  
parent (*l. c.*, pp. 1291 and 1313), the Betic Strait (*détroit bétic*,  
also called Andalusian connection) was dry during the Oligocene,

<sup>1</sup> *Traité de Géologie*, Vol. 2, 1893, p. 1291.

while sea again occupied it in the Miocene, and thus we would have a chance for the African fauna to reach Northern Spain as early as the Oligocene. This connection, however, scarcely amounted to a complete communication of Africa and Europe, since at that time the Oligocene strait to the north of the Iberian Meseta was still in existence, forming a barrier to the further advance of the African fauna. Thus, even under this assumption, a final connection of Africa and Europe was not established until the end of the Miocene, after the second obliteration of the Betic Strait. Subsequently the connection of both continents was again interrupted by the formation of the Strait of Gibraltar; but this belongs to very recent times.<sup>1</sup>

Another tectonic line goes from Northwestern Africa to Sicily and Italy, and is marked by the eastern continuation of the same mountain range that curves in the west from Africa into Southern Spain. This system belongs to Post-Oligocene times, and as a land-bridge apparently underwent repeated changes. Moreover, it is doubtful whether it existed at any time as a complete and solid bridge, but it is represented as such by Scharff (1895, maps pp. 465 and 470) for the Pliocene time,<sup>2</sup> while Neumayr (1890, Vol. 1, p. 330), for the *Lower* Pliocene, gives only a series of islands.

From the above discussion we are to draw the conclusion that—aside from a connection with the Sinic continent during the Upper

<sup>1</sup> Kobelt, W. (*Studien zur Zoogeographie*—"2. Die Fauna der mediterranen Subregion," 1898), arrives at a different conclusion. According to him, the Mediterranean Sea was separated from the Atlantic Ocean in the *Older Tertiary* by a connection of Central Spain with the Atlas mountains (the Sierra Nevada or Betic Cordilleras did not then exist). The Miocene Tethys reached from India to Spain and Central France, but did not communicate with the Atlantic, the connection along the valley of the Guadalquivir being of Pliocene age.

This result is contrary, however, as we have seen, to what is known of the Geology of these parts. Just the opposite is the case. In the *Older Tertiary* the Tethys and the Atlantic were broadly connected, and in the Miocene they still communicated through the Andalusian or Betic Strait, as is positively shown by the presence of Miocene beds there. But in Pliocene times this strait was dry land.

<sup>2</sup> According to Scharff (in 1897, pp. 461 and 466), this bridge belongs to the *Upper* Pliocene and Glacial times. We shall become acquainted below with the evidence for its existence as an actually connecting bridge.

Cretaceous—Africa, for a very long time, was isolated from the rest of the Old World. After it had become disconnected from South America, at the beginning of the Tertiary, it was absolutely isolated, but soon during the course of the Tertiary it became united with Asia and the new continent of Europe. The most important stages in this process were that of the elevation of Western Asia, in the Miocene, and the elevation of the northwestern parts of Africa and southwestern parts of Europe at about the same time.

This has the following bearing upon the origin of the distribution of our freshwater Crustaceans: The African types of the subfamily *Potamoninae* (chiefly the subgenus *Potamonantes*) could not reach Europe before Miocene times, and, on the other hand, an immigration of the Asiatic types (subgenus *Potamon*) into Africa (and Europe) was also impossible before the Miocene and after the destruction of the Madagassian land-bridge in the earlier Eocene.

Whether the alleged fossil species of *Potamon* from the Miocene of Europe indicate this Miocene connection of Asia, Africa and Europe remains doubtful. The lack of African types in the Mediterranean region of the present time, as well as the general absence of a northerly and easterly advance of them (except in the Nile valley, where the immigration no doubt belongs to a very recent period), is opposed to the above assumption, and it is quite possible that these fossil forms do not belong to relations of the *Potamoninae*. It seems that the desert zone of the Sahara already existed in Miocene times, at least that it began to develop at the same time that Western Asia became land, since just this process furnished the conditions for the origin of an arid climate in North Africa and West Asia. On the other hand, we see that a species of the subgenus *Potamon*, belonging to the Indian fauna, advanced in a westerly direction across the new land areas formed in Miocene time, and that it reached by this route Northern Africa (Egypt and Algiers). But the distribution of this species (*Potamon fluviatile*) needs further explanation, since it is also found in certain parts of Europe, and we shall discuss this question in the next chapter.

#### 10. RELATIONS OF EUROPE TO ASIA.

In discussing the distribution of *Potamon fluviatile* in Southern Europe, just referred to, we are also to consider the presence of the genus *Potamobius* in Europe, the area of which is separated from that of the rest of the genus (in Northeast Asia and Northwest

America). The essential point in this respect is the investigation of the geological relation of Europe to Asia.

Europe did not exist as a continent—*i.e.*, as a continuous mass—from the beginning of the earth's history up to about the middle of the Tertiary. Indeed, there was a number of larger and smaller islands in the old Tethys, but they never were connected so as to assume continental shape. To the north, however, we had the large Scandinavian mass, which probably was connected over Greenland with North America, but we shall disregard this possible junction, since our present material, the Decapod Crustaceans, do not furnish additional facts which bear upon it.

The Tethys, as we have seen (p. 367), covered the whole region of the present Mediterranean Sea and extended over Western Asia, reaching, in the older Eocene, not only as far as the Indian Ocean, but in an easterly and northerly direction as far as the eastern side of the Kuen-Lun mountains and the Gobi desert.<sup>1</sup> Subsequently, in the Miocene, the western parts of Asia (from Asia Minor and Syria to India) became land (Neumayr, p. 501), and the Tethys was cut into a western (the present Mediterranean Sea) and an eastern section (forming part of the Indian Ocean). But during this time, and even afterward, the northern and northeastern parts of the old Tethys persisted. The Miocene Mediterranean Sea (Neumayr, 1890, p. 516) sent a strait from the basin of the Rhone river (France) through Switzerland into Austria, which there widened out into the Pannonian basin and in the Upper Miocene became a huge inland sea, the Sarmatian, which was cut off from its former western connection with the Mediterranean and reached from Austria over Southern Russia into the region of the Caspian and Aral Seas (Neumayr, p. 523). To the south of this sea the present Balkan Peninsula, the Ægean Sea and Asia Minor were largely land, but in Eastern Asia Minor a continuation of the Mediterranean Sea approached almost to the Black Sea. The region of the Caucasus mountains was probably sea up to Miocene

<sup>1</sup> In the Kuen-Lun mountains there are, according to Bogdanowitsch (*Geolog. Untersuch. im oestlichen Turkestan*, 1892, Russian. Review in *Neues Jahrb. f. Mineral.*, etc., 1895, Vol. 2, p. 110), Archaic and Paleozoic rocks and traces of Jurassic deposits (coal-bearing strata), and then again marine Cretaceous beds. Thus it seems that these mountains were land since beginning of the Mesozoic times and formed part of the Sinic continent. During the Cretaceous there was a temporary transgression of the sea.

times, as is shown by a continuous series of sediments lying upon Azoic rocks. Here<sup>1</sup> has been found Jurassic, Cretaceous, Eocene, Oligocene and Miocene. The latter deposits (Miocene) belong to the Sarmatian inland sea. Beginning with the Pontic stage, the sea recedes on the southern side of the Caucasus (freshwater deposits), while on the northern side marine deposits, belonging to the Ponto-Caspian Sea, continue. The latter disappear after the Glacial period.

The map, given by Neumayr, of the Eastern Mediterranean countries during the Lower Pliocene (1890, Vol. 1, p. 330, see also Vol. 2, p. 526) exhibits a much more extended development of land than at the present time. Especially striking is the direct connection of Asia Minor with the Balkan Peninsula and Central Europe. The corresponding map for the Later Pliocene, given by Scharff (1895, p. 465, and 1897, p. 461), indicates an additional land connection from Dalmatia over Southern Italy and Sicily to Algiers (see also 1895, p. 470, and 1897, p. 461), which is represented in Neumayr's map only by a series of islands.<sup>2</sup> Thus we obtain a continuous land connection from Asia Minor to North-western Africa, belonging to the Pliocene age.

In the Pleistocene (Glacial) time, according to Scharff (1897, map p. 466), this connection is still present.

In the northern parts of Europe we have no land connection in an easterly direction during the Cretaceous time. According to Koken (1893), however, North Asia was connected with Scandinavia in the *Upper* Cretaceous, forming part of a huge circumpolar Arctic continent; but the evidence for its existence seems to be very doubtful. For the Older Tertiary, Koken again indicates a separation of Northern Europe from Asia. In subsequent times, up to the Later Pliocene, the Sarmatian Sea covered the whole of Northeast Europe (Scharff, 1897, map p. 461), thus perpetuating the separation from Asia. During Glacial times this separation was maintained by the ice sheet covering Northern Russia and by the existence of the Aralo Caspian basin, and it was not until Interglacial times that a communication of Asia and Central

<sup>1</sup> See Fournier, in *Ann. Fac. Sci. Marseille*, Vol. 7, 1896.

<sup>2</sup> The *large* extension of the Mediterranean Sea to the south of Algiers over the Sahara desert in a westerly direction, as shown by Scharff's map (p. 470), is probably erroneous.

Europe was established north of the Aralo-Caspian basin over Southern Russia (Scharff, 1897, map p. 466).

The gradual origin of Europe, beginning with the formation of the chief mountain chains in the Oligocene, its connection first of the southern and central parts with Western Asia across the Balkan Peninsula (Miocene and Pliocene) and with Northern Africa over Spain (end of the Miocene), and subsequently the connection of the central and northern parts with Siberia (over Russia), by which processes Europe assumed the shape of a continent (part of Asia), have been largely used by previous authors for the explanation of the zoogeographical conditions of Europe.

Osborn (1900, p. 569) mentions a repeated immigration of Mammals into Europe and indicates the Upper Eocene, the Miocene and the Pliocene times as most important in this respect. But we must always bear in mind that during the Older Tertiary Europe was not a unit at all—in fact did not exist as a zoogeographical section. The Old Tertiary Mammalian faunas of Europe (chiefly in the Northwest, in France) probably belong to the British-Scandinavian mass, which was connected, as has been mentioned incidentally, with North America.<sup>1</sup> Then, in the Miocene, we have in Europe, which assumes a more consistent shape, a fauna of new character, the origin of which is to be sought in the East and Southeast (Asia), and possibly during this time the first African types reached Europe, either by the roundabout way over Western Asia or more directly over Algiers and Spain.

Kobelt (1897) also assumes an isolation of Europe at the beginning of the Tertiary, and discusses the immigration of an Indo-Chinese fauna from the East in Pliocene times, while the Nile valley formed a route by which freshwater animals immigrated from the South (Africa).<sup>2</sup>

The most detailed investigations on this question have been pub-

<sup>1</sup> As to this connection, which is not treated here, I refer the reader to Neumayr (1890, Vol. 2, pp. 497 and 504) and to Scott (*An Introduction to Geology*, 1897, p. 505).

<sup>2</sup> Contrary to this, Pilsbry (1894) is inclined to assume, for the *Helices*, a Cretaceous immigration from Southeastern Asia into Europe and Africa. But according to the present state of our knowledge, as set forth above, the history of the development of Africa and Europe, as well as of Asia, does not warrant this assumption. There was no possibility, on geological grounds, for the old Sinic fauna to reach Europe and Northern Africa before the Miocene.



lished by Scharff (1897). He distinguishes—aside from an Arctic migration—two main routes of immigration into Europe during the Later Tertiary period: 1, a *southern* one during Miocene and Pliocene, which was directed from Western Asia over Asia Minor, the Balkan Peninsula, Italy, Sicily, Algiers and Spain (and which apparently sent a branch from the Balkan Peninsula into Central Europe), and 2, a *Siberian* migration from Western Siberia through Southern Russia to Central Europe, which belongs to the Pleistocene (see map, *l. c.*, p. 466) and was impossible before this time (in Miocene and Pliocene), the Sarmatian and Ponto-Caspian Sea forming barriers.

Comparing our freshwater Decapods with the above, we see at the first glance that the present distribution of the European freshwater crab, *Potamon fluviatile*, unmistakably agrees with that land connection which began in the Miocene and culminated in the Pliocene and which extends from Asia Minor over the Balkan Peninsula to Italy, Sicily and Algiers. Even the minor features of it are traceable. *Potamon fluviatile* is found everywhere in Western Asia, in the Caucasus region and in the Crimea, but is missing in the rest of Southern Russia. This corresponds to the fact that the Crimea was connected in Pliocene times with the Caucasus and was not in communication with the rest of Russia (see Scharff, 1897, map p. 461). *Potamon fluviatile* is found in Asia Minor, Syria, on the island of Cyprus and in Egypt. All these parts were then connected. Along the tract of the land-bridge, from Asia Minor to Italy and Algiers, this crab has been everywhere found.<sup>1</sup> This relation of the supposed Pliocene land extension with the distribution of *Potamon fluviatile* is so close that there is no objection whatever to the assumption that the immigration of this species falls in the *Upper Pliocene*, when this land connection was fully developed, and not in the Lower Pliocene, when there was only a series of islands (see p. 374).

Turning now to the crayfishes of Europe, we see that the centre of the range of the group of *Potamobius astacus* (the Russian crayfishes) is just in that region which, during Miocene, Pliocene and

<sup>1</sup> That this species extended, in former times, farther to the north from the Balkan Peninsula is shown by the discovery of it in fossil state in diluvial calcareous tufa near Sütő, Com. Komárom, Hungary (see Loerenthey, E., *Not. Hefte Ungar. Nat. Mus.*, 1898. Review in *Neues Jahrb. f. Mineral., etc.*, 1900, Vol. 2, p. 473).

the beginning of the Pleistocene, was covered by the Sarmatian and Ponto-Caspian Sea. This group consequently can only have reached these parts at a later period, namely, in Interglacial or Postglacial times, and its immigration no doubt corresponds to the Siberian of Scharff (*l. c.*, pp. 448 and 466). In regard to the other group formed by the two species, *P. pallipes* and *torrentium*, which occupy the South and West of Europe, we have to call attention to the important fact that this group is found not only in Southern and Western Europe, but also in England. Now we know that England was connected with the continent in Preglacial and even during Glacial times, and that this connection existed up to the beginning of the Siberian migration (Interglacial). It was interrupted later—according to Osborn (1900, p. 572), at about this time (Middle Pleistocene) and possibly even later.<sup>1</sup>

The fact that *Potamobius astacus* is found in France, but not in England, while *P. pallipes* passes over into the latter country, points to a difference in time of the immigration of either species. *P. pallipes* arrived in these parts before the end of the Glacial time, *P. astacus* at the end of it or even later. The latter consequently without doubt belongs to the Siberian migration, but rather to the later part of it. *P. pallipes* may belong to the earlier Interglacial part of the Siberian migration and have come from East and Central Europe; but it is also possible that it belongs to Scharff's southern migration and came from Asia Minor over the Balkan Peninsula. It is true, forms of the *pallipes* group have not been found in Asia Minor nor in Algiers, but it is not impossible that such may be discovered in these parts, or that they once existed there and have now disappeared. We shall see below why this latter assumption is admissible. The crayfishes in Asia Minor, Southern Italy and Algiers may have been exterminated by the freshwater crabs subsequently occupying these parts. Until this question is finally settled it is impossible to decide whether the group of *P. pallipes* has reached its present area by the southern route (Miocene-Pliocene) or by the route of the Siberian migration (end of the Pleistocene); but however that may be it arrived in Europe before the group of *P. astacus*.

The connection of the European crayfishes with the Sinic conti-

<sup>1</sup> Suess (1888, p. 528) thinks it possible that this happened in historic time or shortly before the beginning of it.

ment, where presumably their original home was located, is not yet established. It must necessarily have gone over Central Asia. Crayfishes of the European type are found eastward as far as Turkestan. It is doubtful whether crayfishes are absolutely lacking in the region between Turkestan and the Amur river. None are reported, but these parts are very poorly known. For the present I cannot imagine any reason for their disappearance in this region, in which they must have once existed, and therefore it is well to suspend judgment until these parts have been properly investigated.<sup>1</sup>

## SUMMARY OF RESULTS OF PART II.

### A. HISTORY OF THE CONTINENTS.

#### a. *Lower Cretaceous.* (See Fig. 5, p. 379.)

I. During the Lower Cretaceous there existed a *Sino-Australian continent*, comprising *eastern Asia*, the *Indo-Malaysian Archipelago* and *Australia*, and which was continued to *Antarctica*. We may retain for this continent the name SINO-AUSTRALIAN, although it is larger than that drawn by Neumayr for the Jurassic time. We are justified in doing this, since probably the Jurassic *Sino-Australia* also included Antarctica.

II. Besides, we have a *Nearctic continent*: this consists of the larger part of present *North America*, and extended probably across *Greenland* to the *Scandinavian mass* of North Europe. This continent also corresponds closely to Neumayr's NEARCTICA of Jurassic times, and consequently we have retained this name for it.

III. A third continent was formed by *Central America*, and we shall call this by the name ANTILLIA. Its remnants are now found in *Central America*, the *West Indian Islands* and *northern South America* (excluding Guiana). This continent is not given by Neumayr for the Jurassic, but probably existed then.

IV. A fourth continent was formed by the western portion of old

<sup>1</sup> A theory lately propounded by C. F. Wright (see *Science*, Vol. 16, Aug. 15, 1902, p. 262 f.) would go far toward an explanation of the causes leading to the destruction of the Central Asiatic crayfishes if properly supported. Wright believes that Northern and Central Asia was largely covered by water in recent geological time, but the evidence introduced for this is, in my opinion, entirely inappropriate. Of the five points mentioned by Wright two (Nos. 3 and 4) have no bearing at all upon this theory, and the value of the other three, especially of the fifth, is highly questionable.



Gondwana Land. It comprises the *Brazilian mass* (including Guiana) and *tropical Africa* with the *Lemurian Peninsula* (Madagascar-India). This continent corresponds, generally, to Neumayr's Jurassic *Brasilo-Ethiopian* continent, but comprises a smaller part of South America (also, for Jurassic times, the section of South America that entered it, according to Neumayr, is too large). It agrees to a certain degree with what v. Ihering has called *Archhelenis*, although it is larger, and it may be permitted in this sense to modify the conception of ARCHHELENIS.

Thus in Lower Cretaceous times we have the following four continental masses: *Sino-Australia*, *Nearctica*, *Antillia*, *Archhelenis*, which were mutually isolated. Besides, there were smaller islands, chiefly in the region of present Europe.

*b. Upper Cretaceous.* (See Fig. 6, p. 381.)

The following changes took place:

*Sino-Australia* was divided into a *Sinic* (Asiatic) and an *Australian* part, the latter comprising Australia and Antarctica.

The *Sinic* section of Sino-Australia became united, across Bering Sea, with the *western part of Nearctica*.

The *western part of Nearctica* was separated from the *eastern*.

The *western part of Nearctica* became united with *Antillia*.

*Guiana* became united with *Antillia* and separated from the *Brazilian mass*.

*Brazil* became disconnected from *Africa*.

The *Lemurian bridge* was connected with the *Sinic continent*.

The result of this is:

I. *An irregular ring of land around the earth*, which, generally, encircles it in the direction of the equator, but curving far to the north in the region of the *Pacific Ocean*. This ring, beginning at the *Sinic land*, goes across *Bering Sea* to *western North America*, thence to *Antillia*, *Guiana*, *Africa* and the *Lemurian land-bridge*, which latter completes it by its union with the *Sinic land*. We may call this ring-shaped continent MESOZONIA.

Aside from Mesozonia we have, separated from it, the following continental masses:

II. *UPPER CRETACEOUS NEARCTICA*. Smaller than the Lower Cretaceous continent of the same name, since its western part is cut off and enters Mesozonia.

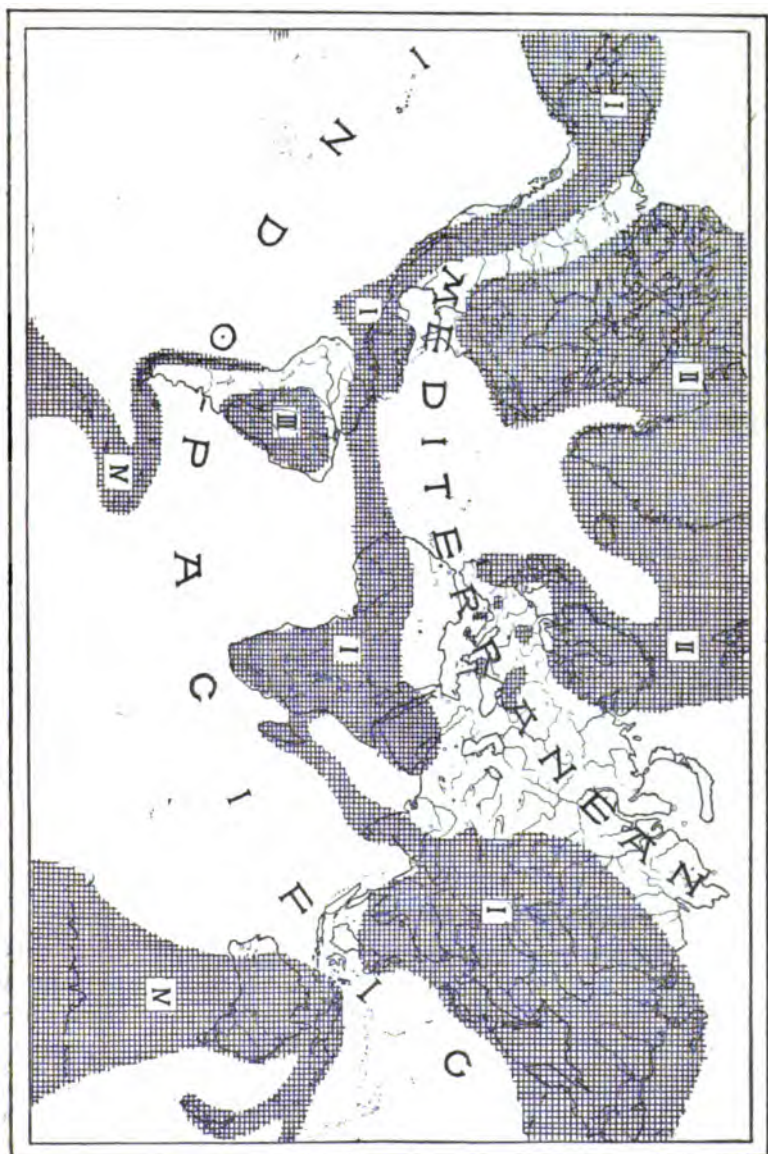


FIG. 6. Distribution of land and water during the *Upper Cretaceous* period.

III. ARCHIPLATA of von Ihering, comprising *Brasil*, south of the Amazonas, and *northern Argentina*.

IV. ARCHINOTIS, comprising *Australia* and *Antarctica*. As will be noticed, the term *Archinotis* (as used by von Ihering and others) does not exactly correspond to the meaning given to it here, but we think it convenient to define this term in this way, applying it only to the truly notal regions; aside from *Australia* and *Antarctica*, a part of *South America* belongs to Archinotis, namely the *western* (Chilian coast range).

*Note*—The existence of this ring-shaped continent *Mesozonia* in Upper Cretaceous times is extremely important for marine zoogeography. The distinction of two types of marine faunas, the MEDITERRANEAN and the PACIFIC, is well known among geologists, and this continent furnishes an explanation for this differentiation: all parts of the oceans lying to the north of Mesozonia—as far as the present knowledge goes—possess the *Mediterranean type*, all parts to the south of it exhibit the *Pacific type*.<sup>1</sup> In subsequent times both types of marine faunas frequently communicated, but there was never a complete fusion of both elements, and finally they developed into the *Atlantic* and *Indo Pacific types* of the present marine fauna, the *Atlantic* being a continuation of the *Mediterranean*. In later Tertiary and recent times the differences of both were again emphasized, chiefly on account of the development of an ARCTIC and ANTARCTIC TYPE through the action of climatic agencies, which prevented their communication in the northern and southern regions of the earth. At present both original types which, as we have seen, go back to the Cretaceous, are restricted to the circumtropical belt, and are absolutely separated.

c. *Lower Tertiary*. (See Fig. 7, p. 383.)

The following changes appear:

The ring formed by *Mesozonia* was interrupted at three places: 1. between *Guiana* and *Africa*; 2. in *Central America* (Panama region); 3. between *Africa* and *Southeast Asia*. This latter inter-

<sup>1</sup> Of course, there are apparent exceptions. The Lower Senonian deposits of western Venezuela possess Mediterranean character (see Gerhardt, *N. Jahrb. Miner., etc.*, Berl., B. 11, 1897), but this is possibly explained by the assumption that they formed part of the Caribbean Sea just formed (see above, p. 343). The Mediterranean character of the Lower Cretaceous of Colombia, Ecuador and Peru is easily explained by the Orinoco strait.

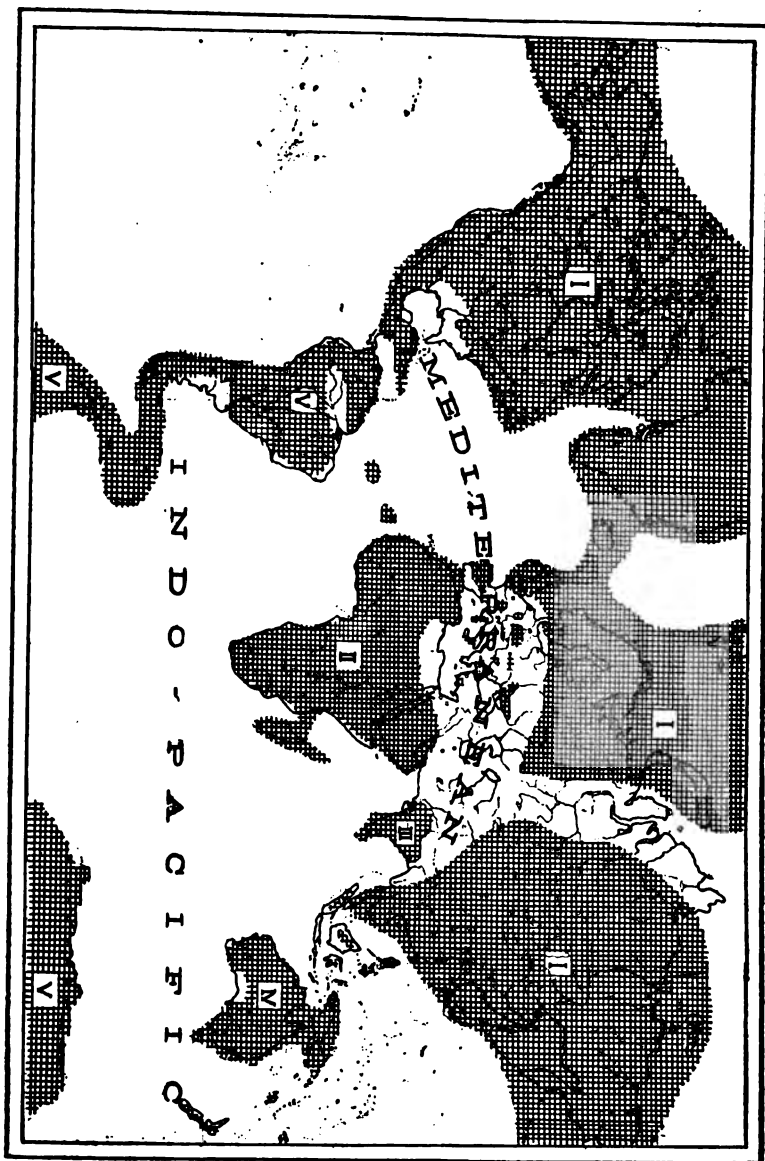


FIG. 7. Distribution of land and water during the *Lower Tertiary* period.



ruption is a double one, the Lemurian bridge between *Madagascar* and *India* being destroyed and *India* becoming again disconnected from the *Sinic land*.

The *southern part of Antillia* (with *Guiana*) becomes united with *Archiplata*.

*Archiplata* becomes connected with *Antarctica*.

*Antarctica* is cut off from *Australia*.

This results in the following five isolated continental masses:

I. *Sino-Nearctic continent*. Composed of the whole of *North America* (including possibly the *Scandinavian mass* in Europe), the northern parts of *Central America* and of *Eastern Asia* (*Sinic land*).

SINO-NEARCTICA comes very near to what von Ihering has called *Archiboreas*, with the exception that Europe does not belong to it. Von Ihering's *Archiboreas* is almost identical with the "*Holarctic region*," only from the latter the "*Sonoran region*" (southern North America) is excluded.

II. OLD TERTIARY AFRICA. This mass nearly approaches to present conditions, but still includes *Madagascar* and *Arabia*.

III. THE INDIAN ISLAND. A very small part, hardly worth the name of a continent, but here so-called in order to emphasize this important stage in the development of southern Asia.

IV. AUSTRALIA, which closely resembles its present form.

V. *Archinotis* and *Archiplata*, together with the *southern parts of old Antillia* (northern South America). This largely represents present *South America* with the addition of the *Antarctic land*. If we are to choose a name for it, we should like to propose NEONOTIS, in allusion to its relation to the older (Upper Cretaceous) *Archinotis* and the *Neotropical continent* of recent times.

d. *Upper Tertiary*. (See Fig. 8, p. 385.)

The following are the most important changes:

*Sino-Nearctica* is greatly enlarged, and becomes connected with the following parts: 1. in the Old World, with the island of *India*, with *Africa*, with the *European Archipelago*, and with *Scandinavia*; 2. the Nearctic part of *Sino-Nearctica* becomes connected, in the region of the Isthmus of Panama, with *Neonotis* (South America).

*Madagascar* is cut off from *Africa*.

*Antarctica* becomes separated from *South America*.

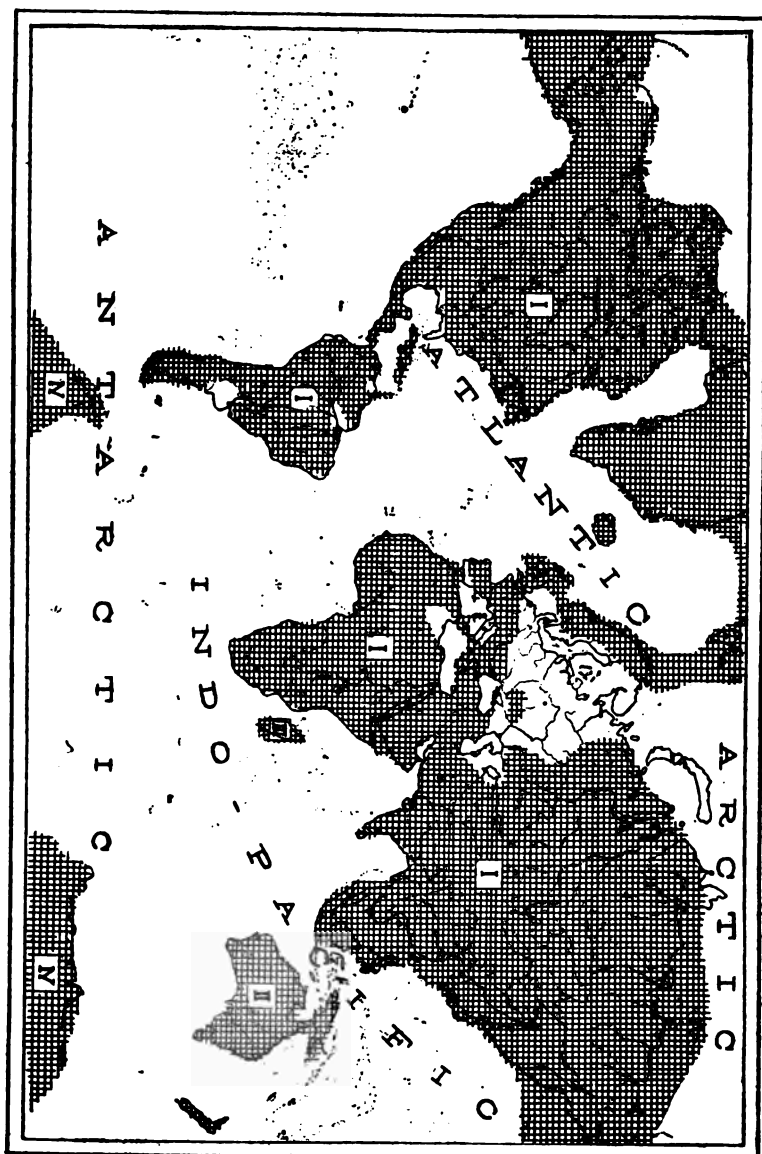


FIG. 8. Distribution of land and water during the *Upper Tertiary* period.

The result is :

I. *One large, continuous, continental mass*, comprising almost all of the *Old* and *New Worlds*. We may call it HOLOGÆA. It is composed, not only of the *Old World*, together with *North America* (*Arctogæa* of previous authors), but also of *South America* (*Neogæa* of previous authors).

Separated from it, we have only the following smaller parts of old continental masses :

— II. AUSTRALIA, which may be regarded as a second continent.

— III. MADAGASCAR, which is merely an island.

IV. ANTARCTICA, which, on account of the deterioration of the climate, loses its character as a centre for the origin of life.

*Note*—Here we have the *greatest continuity* of land masses of the earth that ever existed : practically all parts of the world that are important zoogeographical centres were mutually connected, with the exception of two comparatively small sections, Australia and Madagascar, and the barren regions of Antarctica.<sup>1</sup> This union of old centres of radiation had a very important result : we must attribute to it the fact that the distribution of many continental forms of life has been rendered confused, and the difficulty at the present time in tracing the origin of the different groups. Of course, Upper Cretaceous Mesozonia and other connections of Pre-Miocene times have had their share in effacing many of the original features of distribution, but *Late Tertiary Hologæa is the chief cause of uniformity in distribution* : in most cases "cosmopolitan" distribution, with the exception of Australia and Madagascar, may safely be referred to these Upper Tertiary conditions.

*c. Recent time.*

The most important changes that brought about the present distribution of the continents is the *separation of North America from Asia by Bering Strait, and of North America from Europe*. Thus we obtain a recent zoogeographic division into parts that represent important centres of distribution :

I. *Old World* (Europe, Asia, Africa). This agrees partly with Sclater's *Arctogæa*, except that North America is excluded. We may choose for it the name EUGÆA.

<sup>1</sup> I think that in Late Tertiary times Antarctica was not so desolate and destitute of life as it is now, but there is no doubt that the present character began to develop.

II. *New World* (America). This is *North America* and Sclater's *Neogaea*. I think there is no objection to use *NEOGÆA* for the whole of the "New World."

III. *Australia*. This is Sclater's *NOTOGÆA*.

N. 14 IV. *MADAGASCAR*. Although of small size, the historical development warrants a consideration of Madagascar as a separate centre. In fact, it is—aside from Australia—the oldest isolated part of the world. N. 17

? V. *ANTARCTICA*. This is no longer a centre of radiation; it is now barren of continental life.

*Note*—We claim that this division *solves the problem of zoogeographical research* as indicated by Osborn, and amended in the introduction (see p. 269, footnote 3): *it unites historically and genetically past and present conditions of distribution of continental life*—that is to say, it gives a division that is founded upon the present physical features of the earth's surface as related to life, and pays due attention to the past history of the earth. But this division takes into consideration only the chief *topographical* characters; yet there are others, especially those connected with *climatic* differentiation, which are apt to furnish additional points of view in dividing the earth in zoogeographical units. By using the latter we shall arrive, with only slight changes,<sup>1</sup> at *Wallace's regions*, which, as we have mentioned above (p. 271), are well supported by *physical characters*, although Wallace constructed them according to entirely different principles.

## B. HISTORY OF THE DISTRIBUTION OF CRAYFISHES.

(Compare Fig. 1, p. 275.)

1. In the *Lower Cretaceous* we are to assume that the ancestors of the *Potamobiidæ* and *Parastaciidæ* lived in *Sino-Australia*, possibly extending to its southern extremity, Antarctica.

2. During the *Middle Cretaceous*, *Astacoides* reached *Madagascar* by way of the Lemurian land-bridge, coming from the Sinic continent. Shortly after this, in the *Upper Cretaceous*, the separation of eastern Asia and Australia took place, resulting in the differentiation of the families *Potamobiidæ* (in the Sinic continent) and *Parastaciidæ* (in Archinotis). At the same time, the *Potamobiidæ* extended their range into *western North America*, going as far as *Central America*. Thus, in the *Upper Cretaceous*, the *Potamobiidæ*

<sup>1</sup> This refers to Madagascar.

extended over a great part of *Mesozonia*, from southeastern Asia over northwestern America to southern Mexico, and, in more primitive forms (approaching *Astacoides*), extending even from southern Asia across India to Madagascar.<sup>1</sup>

3. In *Lower Tertiary* times, the genus *Potamobius* gives origin, in *Mexico*, to the genus *Cambarus*, and this spreads over the *eastern parts of North America*. The *Parastacidae* of Archinotis extend from Chili to *northern Argentina* and *southern Brasil*, and the family is divided into an Australian group (which splits up in several genera) and a group belonging to Neonotis (*Parastacus*).

4. In *Upper Tertiary* times (and later), the *Potamobiidae* from eastern Asia reach *western Asia and Europe*, and the *Parastacidae* become restricted to Australia, *New Zealand* and *South America*.<sup>2</sup>

### C. HISTORY OF THE DISTRIBUTION OF FRESHWATER CRABS.

(Compare Fig. 3, p. 297.)

1. In the *Upper Cretaceous*, freshwater crabs of the family *Potamonidae* existed in parts of *Mesozonia*, beginning in India (possibly going eastward to the Malaysian islands), and extending over the Lemurian bridge to Africa, Guiana and Central America.<sup>3</sup>

2. In the beginning of the *Lower Tertiary*, we find this area divided into two main portions. The one comprises *parts of America*: the northern parts of Neonotis and the southern parts of Sino-Nearctica (northern Central America), which are again separated from each other. These regions are inhabited by the subfamily *Potamocarcininae*. The second main portion, occupied by the subfamily *Potamoninae*, is formed by *Africa* and *India*, and this, during this time, is again divided into two sections, an *African* (including Madagascar) and an *Indian*.

3. In the *Upper Tertiary* (and later), the two sections of the range of the *Potamocarcininae* become reunited, so that this subfamily now occupies the *West Indian region, Central America and northern South America*. Also the immigration in the *Lesser Antilles*

<sup>1</sup> The possible cause of the check to the farther distribution of the crayfishes over *Mesozonia*, westward beyond Madagascar and south- and eastward beyond Central America, will be discussed below (see p. 391).

<sup>2</sup> The Madagascar form, *Astacoides*, therefore does not belong to this stock, but should form a group by itself.

<sup>3</sup> It will be noticed that the distribution of crayfishes and crabs in *Mesozonia* is almost mutually exclusive: they came into contact only in Lemuria (and South Asia) and northern Central America. See below, p. 391.

occurred at this time. The *African* stock of the *Potamonina* remains practically unchanged, the *Madagassian* forms alone becoming separated from it; the *Indian* stock spreads over the *Malaysian islands* to *North Australia* and *Japan*,<sup>1</sup> and further, sends out a westward branch over *western Asia*, reaching *Southern Europe* and *Northern Africa*.

#### D. DISTRIBUTION OF *ÆGLEA* AND THE TRICHODACTYLINÆ.

(Compare Fig. 2, p. 296, and Fig. 4, p. 311.)

1. The remarkable resemblance of the range of *Æglea* to that of *Parastacus* suggests identity of origin. This would mean that *Æglea*, in the *beginning of the Tertiary*, inhabited *Chili*, and migrated, at this time, into *northern Argentina* and *southern Brazil*. Since there are no closer relations to this peculiar genus in any other part of the world, *Æglea* apparently is indigenous to *Chili*, i.e., to the northern extremity of the American part of *Archinotis*, and subsequently extended only into the southern part of *Archiplata*. Of course, the opposite direction of migration also is possible.

2. As we have seen above (p. 312) the distribution of the *Trichodactylinæ* offers no remarkable feature. It belongs to the Atlantic slope of present South America (the *Neotropical region* of Wallace) and seems to have formed under the *recent conditions*. Possibly, this subfamily is a new addition to the freshwater fauna, and immigrated from the marine littoral of the Atlantic. Further investigation of this question, together with a closer study of the morphology and systematic relations of this group are very desirable.<sup>2</sup>

#### PART III. CLIMATIC AND BIOGEOENOTIC<sup>3</sup> BARRIERS TO THE DISTRIBUTION OF CRAYFISHES AND CRABS.

In the foregoing discussions we have repeatedly called attention to some distributional facts which we were unable to explain. For

<sup>1</sup> This extension began possibly as early as the Upper Cretaceous and Lower Tertiary.

<sup>2</sup> Everything here depends on the systematic position and affinity of this group. If it should be a primitive one, and really belong to the *Potamonida*, it is possible that it reached Brazil in *Lower Cretaceous* times, when it formed part of *Archhelenis*. Its isolation in *Upper Cretaceous Archiplata*, which was not fully destroyed when it became a part of *Lower Tertiary Neonotis*, would explain its isolated morphological position. In the Tertiary this subfamily would then have extended its range northward.

<sup>3</sup> As to the term "Biocoenotic barrier," compare Ortmann, *Grundsuege der marinen Thiergeographie*, 1896, pp. 41 and 70.

convenient study we may put them together here under the following heads:

1. Explanation of the absence of *Potamocarcininae* in Brazil south of the Amazonas river.
2. Explanation of the absence of *Parastacidae* in Middle and Northern South America.
3. Explanation of the absence of *Astacoides*-like forms in Africa.
4. Explanation of the absence of *Potamobiidae* in Central and South America.
5. Explanation of the absence of crayfishes in Central and South Asia and on the Malaysian islands.

We can dispose of the first point with ease; indeed, we have indicated above the chief cause of it. The *Potamocarcininae* originally (in the Upper Cretaceous) occupied only the region to the north of the Amazonian interoceanic connection. In the Tertiary we have a connection of northern South America with the Brazilian mass (Archiplatea) in the west (region of the Cordilleras), and we see that the crabs availed themselves of this opportunity and spread over the mountainous regions of Ecuador, Peru and Bolivia, possibly here reaching a climatic southern boundary. The Amazonas valley, however, remained sea during a much longer time and was gradually and slowly filled by the deposits carried down from the mountains. Thus, up to a comparatively recent time, it was impossible for the *Potamocarcininae* to cross this depression. That there now exists a possibility of crossing this old barrier is shown by the existence of at least one species on the southern banks of the mouth of the Amazonas near Pará.

In regard to the second point—the absence of *Parastacidae* in the main (tropical) part of Brazil—I can offer no explanation. They must have immigrated into Southern Brazil early in Tertiary times, and possibly we have to deal here with a climatic barrier.

We may take together the other three points, since they apparently are subject to identical causes. Looking at the original distribution of the crayfishes and crabs in Upper Cretaceous times, we have to note the very remarkable fact (see p. 388, footnotes 1 and 3) that both together occupied the whole of Mesozonia, but each different parts of it almost to their mutual exclusion. The crayfishes seem to have existed in the Asiatic part of this conti-

mental ring and in the North American as far as the northern section of Central America. There they gave place to the freshwater crabs, which extended thence to Northern South America, Africa and Lemuria, where they came again into touch with the crayfishes.

The same fact, namely, that crayfishes and crabs are mutually exclusive, holds good for their distribution in recent times. This fact was first pointed out by Milne-Edwards; it has also been mentioned by Faxon, and the present writer<sup>1</sup> has used it for the explanation of some of the features in their distribution. It seems, therefore, that the crabs are more vigorous and active than the crayfishes, and that wherever they came into actual contact the latter were exterminated by the former. It is true there are some countries from which both types of Decapods have been reported, namely, Mexico, Northeastern Australia and Madagascar; but we have no report that both are found associated in the same localities and in the same rivers, streams, ponds or lakes, and it is very likely that just in these regions crabs and crayfishes inhabit stations of a different character. The closer investigation of these conditions would be most interesting.

If we apply this idea, that the presence of crabs forms a biocoenotic barrier to the crayfishes in the former distribution of both, we obtain the following result:

The crayfishes are geologically older than the crabs. They existed, in Lower Cretaceous times, in Sino-Australia, and consequently also in the region of Southeastern Asia and the Malaysian islands. In the Middle Cretaceous they sent a branch (*Astacoides*) across India to Madagascar. But in the Upper Cretaceous the freshwater crabs arrived (or originated) in the same region (Lemuria) and extended into Southern Asia and the Malaysian Archipelago, everywhere exterminating the crayfishes, namely, in India, Southeastern Asia (Farther India and China) and on the islands. They not only acted as a check to the distribution of the crayfishes, but directly annihilated them. Only in Madagascar *Astacoides* survived, probably because in this island it inhabits parts that have not been occupied by the crabs.<sup>2</sup> On the other hand,

<sup>1</sup> See Ortmann, in *Zool. Jahrb. Syst.*, Vol. 9, 1896, p. 593 f., and in Bronn's *Klassen und Ordnungen*, Vol. 5, 1901, p. 1289.

<sup>2</sup> Possibly the large size of *Astacoides* has something to do with its survival. *Astacoides* is—aside from some South Australian species—by far the largest type of all crayfishes.



the original presence of crabs in Africa at about the middle of the Cretaceous would explain the fact that no crayfishes are found on this continent; but, on the other hand, there is the possibility that crayfishes once existed there, but have become extinct on account of the increase of crabs in this country.

Then, again, after the crayfishes had, in Upper Cretaceous times, occupied western North America and Mexico, they met here with the crabs which came from the south, and their farther advance was checked by this biocoenotic barrier.

The question remains, why did the crabs not advance beyond their present (and old) boundaries in China, Australia and Mexico? If it is correct that the existence of crabs forms a barrier to the extension of the crayfishes, the opposite cannot be the case. The presence of crayfishes would not put a stop to a farther dispersal of crabs. But here, I think, we have to deal with climatic barriers. All freshwater crabs are truly tropical animals, entering in only a few cases subtropical countries, but never temperate or cold regions, and thus it seems that the northern boundaries of the *Potamonida* in China and Mexico and the southern in Australia are due to the climate of these respective parts. The same seems to be true in Europe, Western Asia and in Bolivia, where the northern, resp. southern boundaries are apparently given, in a large part, by some features of the climate.

It will be noticed that in applying this principle to the past distribution of the crabs it is necessary to assume the existence, in earlier Tertiary and even Pretertiary times, of climatic differences on the continents, although we do not believe in a climatic differentiation of the oceans of the Mesozoic period. But this is entirely in keeping with our opinion expressed in a previous paper.<sup>1</sup> And, further, I do not mean to say that the present climatic boundaries of the crabs are identical to those of former times. On the contrary, it is quite possible, for instance, that in China the crabs formerly extended farther north, and in Europe we know positively that the European species did so in Diluvial times, reaching as far as Hungary, where it does not now live (see above, p. 376, footnote). The southern boundary of the crabs in Australia, however, seems to be original and has not retreated equatorward, since these

<sup>1</sup> Ortmann, A. E., "An Examination . . . of Climatic Zones in Jurassic Times," in *Amer. Journ. Sci.*, Vol. 1, 1896, p. 270, footnote.

crabs arrived there presumably in a very recent period. Only the boundary in Mexico needs investigation, but possibly here it is not temperature that puts a stop to the northern advance of the crabs, but another climatic factor, namely, the arid or semiarid character of the country lying to the north of the actual boundary, which possibly has existed from the beginning of the Tertiary.

The above considerations would sufficiently explain the third, fourth and partly the fifth points (see p. 390), namely, the absence of crayfishes in Africa, the absence of *Potamobiida* in Central and South America and their absence in South and Southeast Asia and on the Malaysian islands. They could not enter Africa and could not go beyond Mexico on account of the presence of crabs in these parts, and in Southeastern Asia and Malaysia they must have once existed, but have succumbed under the onslaught of the crabs. This latter cause seems also to control the distribution of the crabs and crayfishes in Southern Europe (see p. 377). It does not explain, however, the absence of crayfishes in Central Asia, and, as regards this point, we are unable to offer any reasonable explanation (see p. 378 and footnote).

#### CONCLUSION.

Although we have tried to advance explanations for many of the puzzling facts in the distribution of the freshwater Decapods discussed here, we are to bear in mind that the ideas brought forward are largely hypothetical and tentative. In many respects we have found a wonderful agreement between the distributional facts and what is known about the geology and tectonics of the respective parts, and it was one of my chief purposes to point out that it is possible to more closely correlate zoogeography and geology. But, nevertheless, I am fully aware of the danger that lies in our incomplete knowledge, not only of the geological configuration of the different countries here discussed, but also in the deficiency of the chorological facts at hand.

I wish most strongly to emphasize that I do not believe in all cases to have correctly revealed the ancient relations of land and water, and I think that my ideas of the old continents need confirmation and probably modification. I have only tried to give a representation of what I think of the changes that have taken place during the earth's history, as far as the present state of our knowledge permits of any conclusions in this respect, and I earnestly

wish that my opinions may be investigated by other authors and compared with material furnished by other groups of animals, as well as with more complete and reliable geological observations to be made in future. The way in which such investigations should be carried on has been indicated in this paper.

Finally, I want to point out that most of the ancient continental connections here discussed are not treated for the first time, but have been hinted at or more or less closely investigated by previous authors, zoogeographers as well as geologists. But, unfortunately, the former have not generally paid much attention to the results obtained by the latter, and *vice versa*. Just this lack of a broader view, chiefly among zoogeographers, has induced me to attempt to harmonize both sets of facts, and the results here presented are possibly apt to serve as an apology for having undertaken this task although much preliminary work remains to be done.

#### APPENDIX.

##### RELATION OF THE MARINE DECAPOD FAUNAS OF THE EASTERN AND WESTERN SIDES OF TROPICAL AMERICA.

We have mentioned above (p. 359, footnote) that the facts furnished by the characters of the marine faunas of either side of Central America are frequently misunderstood or misrepresented. In order to get at a proper understanding of the relations of the Atlantic and Pacific Oceans, as revealed by these facts, I shall endeavor here to give a (incomplete) list of identical, resp. closely allied forms of Decapod Crustaceans, which are especially apt to throw a light on this question.

I have made it a point to include in this list only such forms as give plain and unmistakable indications in this respect, that is I have used only those cases in which the relations between the Panamic and Caribbean region are the closest known, which, generally, is self-evident only when the respective forms (mostly species of the same genus) are not known outside of American waters. In genera or groups, where representatives are also known from other parts (especially the Indo-Pacific region), it is not always easy to determine the relation of the different forms, and the question whether the West and East American forms are the most closely allied ones remains unsettled: therefore I shall disregard such instances.

Nevertheless, I am able to offer here a list that is quite large.<sup>1</sup>

PACIFIC SIDE.	ATLANTIC SIDE.	REMARKS.
<i>Panulirus interruptus</i> (Rand.).	<i>P. argus</i> (Latr.).	The Californian species is <i>the</i> most closely allied form, although the genus is circumtropical.
CALCINUS TIBICEN (Hbst.), Ecuador (Nobill, <i>Boll. Mus. Torino</i> , Vol. 16, 1901, p. 26).	C. TIBICEN (Hbst.).	
PETROLISTHES GALATHINUS (Bosc.).	P. GALATHINUS (Bosc.).	We exclude <i>P. armatus</i> Gibb. as a circumtropical species.
PACHYCHELES PANAMENSIS Fax. (see Nobill, <i>l. c.</i> , p. 19).	P. PANAMENSIS Fax.	
Genus <i>Lepidopa</i> .	Genus <i>Lepidopa</i> .	Number of species doubtful, but exclusively found in the West Indies and Low. California. The species on both sides different.
<i>Remipes strigillatus</i> Stps.	<i>R. cubensis</i> Sauss.	Also in West Africa. This group of the genus is found nowhere else. The genus is circumtropical.
<i>Albunea lucasia</i> (Sauss.).	<i>A. gibbesi</i> and <i>pareti</i> .	No other species of the genus are so closely allied, although the genus is circumtropical.
HIPPA EMERITA (L.).	H. EMERITA (L.).	Genus circumtropical.
<i>Hypoconcha panamensis</i> Sm.	<i>H. sabulosa</i> (Hbst.). <i>H. arcuata</i> Stps.	Genus found nowhere else.
ETHUSA AMERICANA A. M.-E.	E. AMERICANA.	Genus cosmopolitan.

<sup>1</sup> Where no references are given, the facts are taken from Ortmann, in Bronn's *Klass. u. Ordn.*, Vol. 5, 1900, p. 1275, and from my unpublished revision of the respective groups for the "Thierreich."

Identical species are printed in SMALL CAPITALS; the most important forms, where the genus is not found outside of American waters, are printed in *italics*.

PACIFIC SIDE.	ATLANTIC SIDE.	REMARKS.
<i>Ranilia angustata</i> Stps.	<i>R. muricata</i> M.-E.	<i>Ranilia</i> M.-E. includes <i>Notopus</i> d. H. and <i>Raninops</i> A. M.-E. The species mentioned here form a natural group, which is not found elsewhere.
<i>R. fornicata</i> (Fax.).	<i>R. stimpsoni</i> (A. M.-E.). <i>R. constricta</i> (A. M.-E.).	
<i>Lithadia cumingi</i> Bell. <i>L. digueti</i> Bouv.	<i>L. cariosa</i> Stps. <i>L. miersi</i> Ortm. <i>L. cadaverosa</i> Stps. <i>L. cubensis</i> Mrls. <i>L. pontifera</i> Stps.	This genus is found nowhere else.
<i>Uklias ellipticus</i> Stps.	<i>U. limbatus</i> Stps.	Genus found nowhere else.
<i>Persephona subovata</i> (Rthb.). <i>P. orbicularis</i> Bell. <i>P. edwardsi</i> Bell (= ? townsendi (Rthb.)).	<i>P. punctata</i> (L.).	Of one species ( <i>P. lichtensteini</i> Leach) the habitat is unknown, but it is certainly from America. The genus is not found elsewhere.
<i>Hepatus chilensis</i> M.-E.	<i>H. epheliticus</i> (L.). <i>H. annularis</i> (Ol.).	Several doubtful species, but none outside of American waters.
<i>Hepatella acina</i> (Stps.). <i>H. lavis</i> (Rthb.). <i>H. lata</i> (Fax.). <i>H. amica</i> Sm.	<i>H. tuberosa</i> (Stps.).	<i>Hepatella</i> — <i>Osachila</i> . One species, <i>H. stimpsoni</i> (Stud.), at Ascension Island. No other species from any other part of the world.

The following are taken from Rathbun, *U. S. Nat. Mus.*, Vol. 15, 1892:

<i>Pericera triangulata</i> Rthb. <i>P. configua</i> Rthb.	<i>P. cornuta</i> (Hbst.). <i>P. atlantica</i> Rthb.	Genus found nowhere outside of America.
<i>Othonia nicholsi</i> Rthb.	<i>Othonia</i> (4 species).	Genus not found outside of America.
<i>Mithrax</i> (4 species).	<i>Mithrax</i> (14 species).	Genus not found outside of America.

The following are taken from Rathbun, *U. S. Nat. Mus.*, Vol. 16, 1893: N. 13

PACIFIC SIDE.	ATLANTIC SIDE.	REMARKS.
<i>Libinia macdonaldi</i> Rthb.	<i>L. spinimana</i> Rthb.	Other species known from both sides, and possibly from other parts of the world, but these two are especially closely allied.
<i>Pelia</i> (2 species).	<i>Pelia</i> (2 species).	Genus found nowhere else.
<i>EPIALTUS BITUBERCULATUS</i> .	<i>E. BITUBERCULATUS</i> .	There are four other species on the Pacific side. The genus is found nowhere else.

The following is taken from Rathbun, *ibid.*, Vol. 18, 1896, and *Proc. Biol. Soc. Wash.*, Vol. 10, 1897: -N. 13

<i>Callinectes</i> (4 species).	<i>Callinectes</i> (6 species).	All Pacific species different from the Atlantic. Three of the Atlantic species also found in West Africa. Genus not found elsewhere.
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The following is taken from Nobili, *Boll. Mus. Torino*, Vol. 16, 1901, p. 32:

<i>CRONIUS RUBER</i> (Lmck.)	<i>C. RUBER</i> .	This species also in West Africa, but nowhere else.
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In this list we see there are *seven identical species*. The rest are more or less closely allied, but the affinity is always so close that it is not equaled in any other part of the world, with the exception of West Africa, where some of the types have been found that are common to the east and west sides of America, but are lacking everywhere else. This affinity of the West African littoral fauna is a well-known fact, and there is nothing remarkable about it, since a communication between both sides of the Atlantic is possible in many cases even at present times.

Aside from this, a close relation of the western and eastern faunas of the Central American shores is revealed at a glance.<sup>1</sup> Hill says (*l. c.*, p. 267) that the recent faunas of the opposite sides of the isthmus are so distinct that the communication of waters must have belonged to a very remote time, and that there has been probably no communication since Miocene. We may modify this a little and say that the affinities of the Decapod fauna of the Atlantic and Pacific are unmistakable, and *that we have ample and convincing evidence that there must have once been a connection.* The scarcity of identical forms (which in part are not beyond doubt), and the demonstrated fact that generally one (or more) species of the respective genera replace each other on either side of America, being distinctly different, although closely allied, shows conclusively that this connection cannot have been of a very recent date. I think that the Decapods confirm Hill's opinion that *there was no communication whatever of both oceans since Miocene time*, and we may add that probably the similarity of both faunas is to be referred in most cases to the Eocene and Oligocene interoceanic connection across the isthmus. After this had been closed sufficient time has elapsed to generally change the characters of the once identical Pacific and Atlantic stock and to render them different species, while only a few have preserved their original characters and are to be regarded as identical species.

Of course it is possible that some of the similarities of the Pacific and Atlantic faunas go back to earlier (Mesozoic) times, when the

<sup>1</sup> In speaking of a close resemblance of these faunas, I wish to avoid being misunderstood. There are cases that show a close resemblance, but this does not mean that both faunas are closely related in *all* respects; on the contrary, there are other elements on both sides of Central America that are peculiar to only one of them. The Panamic fauna, for instance, contains Indo-Pacific elements and a very peculiar element that belongs to the whole western coast of America (from the Western United States to Chili). I have called attention to this element in a former paper (*Zool. Jahrb. Syst.*, Vol. 9, 1896, p. 582 ff.), but I have been entirely misunderstood by von Ihering, who says (*Rev. Mus. Paulista*, Vol. 2, 1897, p. 379) that my theory of a migration along this coast is disproved by the fact that different faunas succeed each other along this coast from the south to the north. This is quite true, but it does not disprove my theory, since I never meant to say that the whole of the West American fauna has reached these parts by migration from north to south or *vice versa*. On the contrary, only a part of it belongs to this category, and there are other components of the West American fauna which came from quite different sources.

Mexican, Orinoco and Amazonas interoceanic connections existed. But this would not influence our general result that the communication of the oceans was interrupted definitively in the Miocene.

We have, beginning in Mesozoic times, a differentiation of two types of marine faunas, a Mediterranean and a Pacific, but these faunas communicated with each other at certain points and were completely separated for a comparatively short period in the Upper Cretaceous by the continent of Mesozonia (if this separation was at all complete at any time).<sup>1</sup> Generally the Mediterranean fauna belongs originally to the northern hemisphere, the Pacific to the southern, except that the latter largely encroached upon the former in the region of the Northern Pacific. This arrangement was completely upset during the Tertiary, so that at present the Atlantic fauna (containing chiefly the descendants of the old Mediterranean types) and the Pacific fauna are divided, not by a line running east and west, but by two lines running generally north and south (in America and in the Old World). Besides, the Arctic and Antarctic types have been added, the former being an offshoot of the Mediterranean, the latter of the Pacific type.<sup>2</sup>

While in former times, in the Mesozoic and Lower Tertiary, a decided tendency prevailed to mix the marine faunas of the world and make them more or less uniform, which tendency was checked only temporarily, we have, from the Miocene upward, a complete separation of two marine types of fauna,<sup>3</sup> which, however, still possess certain features in common that are due to conditions prevailing in earlier times, and with respect to Central America these conditions (interoceanic connections) were present for the last time in the Older Tertiary (Eocene and Oligocene).

<sup>1</sup> We possess evidence that Mesozonia was interrupted for shorter periods within the Upper Cretaceous, for instance, in the region of British Colombia (see Koosmat) and in Western Venezuela (see above, p. 343).

<sup>2</sup> In opposition to the belief of some authors (Pfeffer, Murray) that both Polar faunas are strikingly similar, I have always held the opinion (see review of the literature in *Americ. Natural.*, Vol. 35, 1901, p. 139 ff.) that this is not so. We see here also that the origin of these faunas is different, the one being derived from the old Mediterranean, the other from the old Pacific fauna, the differences of which, although obscured during the earth's history by frequent interchanges, go back to Mesozoic times.

<sup>3</sup> The complete separation was brought about not only by topographical factors, but chiefly by the additional action of climatic differentiation. See Ortmann, *Grundriss der marin. Tiergeograph.*, 1896, p. 40.



It is a very remarkable fact that the interoceanic connection of the Mediterranean and Pacific type of marine faunas, existing in Western and Southern Asia (Tethys and Strait of Bengal), was ended at about the same time, in the Miocene, by the elevation of Western Asia and its union with Africa and Europe.

PRINCETON UNIVERSITY.

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*Stated Meeting, October 3, 1902.*

Dr. HAYS in the Chair.

A letter was read from Prof. Silvanus P. Thompson, of London, accepting membership.

The decease of the following members was announced :

Ferdinand J. Dreer, at Philadelphia, on May 24, 1902, æt. 90.

Prof. Rudolph Virchow, at Berlin, on September 5, 1902, æt. 80.

Major John W. Powell, at Haven, Me., on September 23, 1902, æt 68.

The following papers were read :

"On a Specialized Cocoon of *Telea polyphemus*," by Prof. A. Radcliffe Grote.

"On Some Aboriginal Languages of Queensland and Victoria," by Mr. R. H. Mathews.

## A SPECIALIZED COCOON OF TELEA POLYPHEMUS.

BY A. RADCLIFFE GROTE.

(Read October 3, 1902.)

The peculiarities of the cocoon of *Telea polyphemus* are well known to lepidopterists. It is of an egg-shape, woven free in the leaf, close and tough in texture, without any false stem or attachment to the tree, deciduous. Among a quantity of Attacid cocoons, received from an old and valued friend of mine in New York, was one which I took at first to belong with the suspensory cocoons of *Philosamia*, among which it came. It was provided with a silken pedicel, 45 mm. in length, which had been spun entirely around the stem of the leaf, not on one side only, and so that the dried stem was enclosed and preserved within. This silken attachment had evidently been shortly fastened above to the branchlet, as is the case with the cocoons of the more specialized Attacid genera, and *Antheræa anylitta*. But the cocoon itself was in this instance far too large and heavy for that of *Philosamia*, and, on examining it closely, it was found to be of a firm, leathery texture, while the chalky-white appearance, which the cocoon of *Telea* presents, could, though with some difficulty, be detected.

All doubts were removed by the appearance, on June 8, of a large female specimen of *Telea polyphemus*, of the ordinary olive-ochre type, a little more intensely colored than usual, but presenting no variation in marking. Now *Telea* does not habitually fasten itself to the leaf and branch in this manner, spinning no false stem or attachment. What circumstances induced this individual to make a singular departure from the habit and custom of the species?

All departures are interesting. This one is particularly so, in view of the ascertained progression in specialization of the Attacid cocoons. Here is an instance of the sudden acquirement of the attachment or pedicel, so that one is led to speculate on the exciting cause. For this purpose a knowledge of the larva, tree, leaf and weather seems necessary, while I have only the moth and the cocoon. But I have elsewhere shown that the specializations of the three states of the Lepidoptera manifest themselves independently. They do not keep exact time in their progression, nor do they move with equal foot, though a general correspondence in direction may be evidenced.

In my work on the Saturnians or Emperor Moths, pp. 15-16, published by the Roemer Museum in June, 1896, I tried to correlate the spinning of an attachment with the increasing breadth of

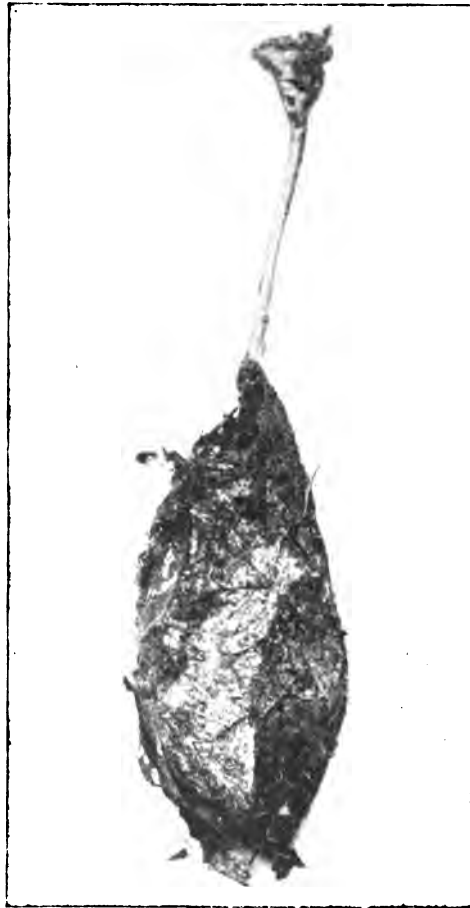


FIG. 1. Cocoon of *Telea polyphemus* with attachment.

wing in the perfect insect. Evidently these large-winged creatures experience the same difficulty in rising from the level ground as do the bats and the swallows. To fly, they must feel the air beneath their wings. It thus became an object, or an advantage,

that the moth should emerge from the cocoon in the high air whence to take its flight. This emergence at an elevation was effected by the spinning of a silken stem, attaching the cradling



FIG. 2. Ordinary cocoon of *Telea polyphemus* without attachment.

leaf permanently to the tree, so that the cocoon could not fall with the dropping of the leaf in the autumn, safely swinging despite the wintry winds. This custom of the larva has become fixed in the arboreal Attacid genera *Philosamia*, *Attacus* and in *Callosamia*

*promethea*. *C. angulifera*, which seems the older form of *Callosamia*, has not acquired the habit. The most generalized group of the ATTACIDES (= *Saturnides* Boisd. 1840, *Saturnina* Dyar, 1894), namely the Aglians or Citheronians, make either a slight cocoon on the surface or none at all, entering the ground to pupate like the Hawk Moths. In the Emperor Moths, specialization of the pupal protection or envelope is evidenced by its growing complexity. *Telea* is one of the genera using a leaf as a wrapper or external support for the cocoon. Neither *Samia* or *Saturnia* have this habit, spinning against stems or branches.

Another advantage arising from the spinning of the cocoon on the tree which served as a food-plant for the larva would be that the perilous descent of the latter down the trunk, to spin in fallen leaves on the ground, is obviated. The habit of descending the tree to pupate appears to be general, and I have observed it with *Actias luna*, which spins a thinner, more papery cocoon than its more specialized ally, *Telea polyphemus*; the cocoon of the latter could probably resist injury to the chrysalis in falling with the leaf.

The specimen of *Telea* here under observation is a remarkably large and heavy one, so that it might be thought possible the larva hesitated to trust to the leaf alone, and hit upon the plan of fastening itself by a silken rope. As against this idea might militate the fact that the forms which habitually attach the cocoon in this manner are relatively light-bodied species, in comparison with their enormous wings. The heavy-bodied species of *Samia* and *Telea* spin no attachment. This latter seems feebly indicated in the cocoon of *Rothschildia iacobææ*. However, the nature of the food-plant may besides hasten or retard the acquirement of the custom, which seems to grow out of the use of a leaf as an outer wrapper, and to correlate with the arboreal habit of the moth.

Whatever opinion we may form regarding the case in point, it is evident that the spinning of the pedicel is not only an advance or a specialization upon an earlier plan of cocoon-making, but that it can be suddenly put forth on occasion by the more generalized or primitive tree-feeding Attacids, as is now demonstrated. And from this instance we may certainly conclude that the habit of spinning a stem to the cocoon has arisen singly, with the leaf-spinning individual, called forth by whatever exciting cause. Out of this individual departure a custom and habit for the species at large has been most probably secondarily developed, since it clearly proved

advantageous to the insect and for the reasons given by me above. So that perhaps in the future both *Telea* and *Actias* may become in this way sessile. And perhaps, when we grasp all the facts which arise in connection with cocoon-making, we may be disposed to recognize in caterpillars, these lowly organisms, an intelligence in so far akin to our own, as it is evidently based upon an identical perception of external conditions. We are here at the simple sources of Mind in Nature.

#### HERMAPHRODITE OF SAMIA CECROPIA.

The occurrence of hermaphroditism or gynandromorphism in the Emperor Moths is sufficiently rare. I may record the fact here that an example of *Samia cecropia* disclosed on June 3, in which the left side, antenna, both wings, and abdomen, so far as can be externally observed, is female, while the right side is as completely male. On the right side the male abdominal clasper can be seen, wanting on the left, so that we have to do with a true hermaphrodite. Incompletely formed eggs were extracted from the left abdominal opening under pressure.

#### LITERATURE ON THE EMPEROR MOTHS.

- 1874. List of the North American Attaci. *PROC. AM. PHIL. SOC.* (Nov., 1874).
- 1895. Notes upon the North American Saturnina with List of the Species. *Canadian Entomologist*, 263 (September).
- 1895. Supplementary note to the Saturnians, *id.*, 316.
- 1896. Die Saturniiden (Nachtpfauenaugen). *Mittheilungen a. d. Roemer-Museum*, No. 6, June. With three photographic plates and eighteen text illustrations.
- 1896. Die Nachtpfauenaugen mit besonderer Berücksichtigung ihrer Flügelbildung. *Verh. Deutsch., Ges. Nat. u. Aerate*, Frankfurt, p. 197 *et seq.* With eleven text illustrations.
- 1896. Note on *Samia californica*. *Journ. N. Y. Ent. Soc.*, p. 201.
- 1897. Classification of the Saturniides. *Journ. N. Y. Ent. Soc.*, pp. 44 *et seq.*  
[I would also draw attention here to an interesting paper by W. T. Davis on Intelligence shown by Caterpillars, *id.*, Vol. V.]
- 1898. The wing and larval characters of the Emperor Moths. *Proc. So. London Ent. and Nat. Hist. Soc.* With four figures in text.
- 1902. An aberration of *Actias luna*. *Can. Ent.*, 70, Vol. 34.

ROEMER MUSEUM, June 14, 1902.

*Stated Meeting, October 17, 1902.*

Dr. HAYS in the Chair.

A letter was read from Dr. R. H. Alison, resigning membership.

The donations to the Library were laid upon the table, and thanks were ordered for them.

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*Stated Meeting, November 7, 1902.*

President WISTAR in the Chair.

The donations to the Library were laid upon the table, and thanks were ordered for them.

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*Stated Meeting, November 21, 1902.*

Mr. RICHARD WOOD in the Chair.

The list of donations to the Library was laid on the table, and thanks were ordered for them.

The decease of the following members was announced :

Prof. Ogden N. Rood, at New York, on November 12, 1902, æt. 71.

Mr. George Harding, at New York, on November 17, 1902, æt. 76.

Dr. Julius Platzmann, of Leipzig.

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*Stated Meeting, December 5, 1902.*

President WISTAR in the Chair.

The list of donations to the Library was laid on the table, and thanks were ordered for them.

The decease of the following members was announced :

Samuel Timmins, F.S.A., at Birmingham, England, on November 12, 1902, æt. 76.

Joseph Miller Wilson, at Philadelphia, on November 24, 1902, æt. 64.

Dr. Alfred Stengel read a paper on "Specific Precipitins and Their Medico-Legal Value in Distinguishing Human and Animal Blood."

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### SPECIFIC PRECIPITINS AND THEIR MEDICO-LEGAL VALUE IN DISTINGUISHING HUMAN AND ANIMAL BLOOD.

BY ALFRED STENGEL.

(Read December 5, 1902.)

Recent studies of the complex problem of immunity have been most fruitful of results, not alone in the direction of explaining immunity, but also in disclosing a number of phenomena whose bearing on the general question is perhaps subsidiary, but whose scientific and often practical interest in other directions is highly valuable. Among these the phenomenon of precipitation is an important one, and it is to this that I desire to direct attention. Kraus first showed that the serum of animals immunized against cholera causes a flocculent precipitation in the filtrate from cholera cultures, while sera from normal animals produces no such results. Later he showed that this precipitation is specific in the sense that cholera serum produces precipitation in the filtrate of cholera cultures alone, while sera from animals immunized with other cultures had no such result. Subsequent investigations have confirmed and extended Kraus' contribution. The peculiar substance which produces the precipitation in the bacterial culture is probably a product of cell activity made under the stimulus of the immunization, and the precipitable body in the cholera culture is extracted from the bodies of the bacteria themselves. It is seen then that this phenomena of precipitation as applied to bacteria is a valuable one in determining bacterial species, but it has not been so employed by bacteriologists, since it is far less easy of application and far less certain in its results than the agglutination test of Gruber, Durham and Widal.



Ehrlich's attractive theory of immunity, which he calls the Side Chain Theory, explains the development of immunity and other problems connected with this question far more satisfactorily than any previous hypothesis. He has shown very clearly that the immunizing substances are products of cell activity under the stimulus of the bacterial toxins, but he has also called attention to the fact that the principle involved in this elaboration of immunizing substances does not differ greatly from that which obtains in the case of the ordinary process of nutrition of cells. In other words, there is a chemical union of the nutrient substance with the cell body in the case of assimilation of food and a similar chemical union in the case of bacterial toxins. The molecular radicals, which have a special affinity for the nutrient body or for the toxin, are entirely comparable to the replaceable atomic groups of organic compounds, such as the benzol ring, and may be displaced from the central nucleus. Being products of the vital activity of the cell, reproduction of such atomic groups is possible, and indeed, according to a well-known principle of pathology, destruction of the atom groups occasions a replacement in excess, attended with a separation from the parent nucleus and extrusion from the cell of the atomic group. When toxins unite with cells the combining radicals or "groups" of the latter are utilized or in a sense destroyed and the cell produces new groups in excess—some or all of which are extruded into the circulation. These liberated groups constitute antitoxin in the case of immunity, and I refer to them here not from any bearing on the question of toxic immunity to our present discussion, but to develop the point that the production of such bodies is a question of chemical nature, and that it does not necessarily involve the action of a living germ. This is proved on the one hand by the production of antitoxic substances by the introduction into the organism of inorganic or organic compounds, and on the other hand by the fact that similar substances are produced when food stuffs and various other organic substances are injected. This is true in particular of the substances concerned in precipitation, and Ehrlich in his later writings has made a strong point of the similarity in the phenomena of precipitation and of bacteriolysis in so far as the origin and essence of the active agents in question are concerned.

To come more immediately to the subject, it has been found that injections of milk, albuminous liquids of other sorts and compound mixtures like urine and blood serum, when introduced into the

animal body, generate or cause the generation of substances which in a more or less specific manner precipitate the substance or compound used in the inoculations. This was first demonstrated in the case of milk by Bordet, who found that when he injected rabbits with sterilized milk and repeated the injection at short intervals the blood serum of the animals subsequently caused precipitation of the milk, while normal serum had no such action. Later it was found by other experimentors that this precipitation is more or less specific, and the serum of a rabbit treated with cow's milk contains a precipitin for cow's milk and not for the milk of other animals, while the serum of animals treated with goat's milk is similarly specific. The same experiment was performed with human milk and the result was similar. The method of carrying out these experiments was as follows: The rabbits were inoculated subcutaneously or intraperitoneally at intervals of several days with sterilized milk, the quantity varying between 10 and 50 c.c. The sterilization was accomplished by heating for an hour at 65° C. or by the use of chloroform. Other rabbits were treated with milk of different sorts as controls. After the treatment had been repeated for a number of times and each rabbit had received about 100 c.c. of milk the serum was obtained by bleeding the rabbit and allowing the blood to coagulate. The serum diluted with four or five times its bulk of water was mixed with milk diluted 1 to 40 and the mixture allowed to stand for some hours. The precipitation was then observed in the milk corresponding with that with which the animal furnishing the serum had been treated.

A very similar series of experiments has been performed with egg albumin. Repeated injections of raw egg albumin cause the development in the blood of a more or less specific precipitin. When crystallized egg albumin was used a specific precipitin was developed. This precipitates the egg albumin, but not globulin, and on the other hand, when serum globulin is used in the injections, the precipitin has no effect upon egg albumin. In the case of these more narrowly specific tests the results have been somewhat at variance. Thus it was found that the serum of animals injected with globulin obtained from bullock's serum had some effect upon blood corpuscles of fowl and also an effect upon sheep globulin. Other instances of non-specific action might be cited, but this one reference is sufficiently illustrative of all.

My own experiments in conjunction with Dr. C. Y. White in

this direction have been made with fresh egg albumin. Taking the white of fresh hen's eggs, we injected from 10 to 15 c.c. into the peritoneal cavity of rabbits. No striking effect resulted from the injections, which were repeated at intervals of a day or two until the rabbit had received from six to ten injections. At the end of that time the serum of the animal was found to precipitate diluted solutions of egg albumin in a striking manner. The same serum had no effect upon serum albumin and globulin contained in the blood of man or various animals, but was not specially tested regarding its behavior toward the albumin of other than hen's eggs. Uhlenhuth, who has experimented in this manner, found, however, that the precipitin is not specific, since the serum obtained from animals immunized with hen's eggs reacts toward pigeon's eggs. He found, however, as we did, that this serum did not react with peptone, casein, blood serum, etc.

Experiments similar to the above were made by Leclainche and Vallée, who injected albuminous urine, and Zülzer, whose work was practically the same. Mertens and Tchistovitch used eels' serum and placental blood serum respectively and found results similar in character to those already detailed.

The most interesting line of work, however, is that done by Uhlenhuth and repeated or elaborated by Wolff, Stern, Wassermann and Schütze, Dieudonne, Nuttall, as well as by myself and Dr. C. Y. White. These experiments concern themselves with the production in the blood of specific precipitins for heterologous blood, and these have been utilized to a certain extent in the determination of diseased conditions or more particularly for the differentiation of human and animal blood.

The manner of procedure in the preparation of the serum is as follows: Rabbits (which have been found to be the most suitable animals) are injected interperitoneally with blood serum or with defibrinated blood. About 10 c.c. is injected at intervals of from two to three days until from five to eight or ten injections have been given. The serum may be utilized immediately after the last injection or the animal may be allowed to rest for a week before its blood is drawn. The blood is then taken after killing the animal or a small quantity may be obtained by bleeding after etherization from one of the large blood vessels. The serum is collected after separation of the clot. Fresh blood may be tested directly with the serum by diluting the blood (1 : 100) with isotonic salt solution.

The solution is made by first diluting the blood with distilled water and then with an equal quantity of double isotonic salt solution. If the diluted blood is not perfectly clear, it is allowed to settle and the supernatant blood is tested. A few drops of the serum of the immunized rabbit are added to the clear solution of blood in a narrow test-tube and a precipitation is generally observed at once or may form after standing for a short time. A later test may be performed by allowing the serum to flow down the sides of the tube under the diluted blood, when a haziness at the point of contact indicates the formation of a precipitate. The precipitate increases somewhat after its first formation, especially when the fluids are kept at 37° C., but precipitates formed twelve to twenty-four hours or more after the mixture is made should be regarded as doubtful. The same form of test may be applied with dried blood. In this case care must be taken in making solutions of the blood stains. The blood stains may be dissolved with normal salt solution, or in the case of old blood stains the method of Ziemke may be employed. In this method concentrated solution of potassium cyanide is used as a solvent. The mixture is shaken with a few granules of tartaric acid until it becomes almost neutral to litmus paper and then filtered. The mixture is diluted to a yellowish-red color and the serum of the rabbit is then added. Solutions of soda have also been used for extracting the blood clot. Uhlenhuth demonstrated the reaction in blood (1) dried for three months, (2) allowed to undergo decomposition for three months, (3) washed with weak alkaline soap, (4) frozen in snow for fourteen days at 10° C., and in (5) blood solutions in which the hemoglobin was changed to carbon oxide hemoglobin.

This test has been confirmed in more or less detail by investigators in all parts of the world and may said to be fairly established, though the limits of its usefulness cannot as yet be drawn with precision. My own experiments with Dr. C. Y. White have constituted injections of a number of rabbits with defibrinated human blood and with blood squeezed from placenta. In both series of experiments, after from five to eight injections, we found the blood serum markedly active in precipitating diluted human blood and without effect upon the blood of dogs, horses and cattle. The first effect of adding the serum was the production of a flocculent precipitate, which invariably increased after a short time. We dis-

carded the mixtures after a few hours, as we had always observed that flocculent precipitation occurred in many of the test-tubes containing other than human blood after a lapse of twenty-four to forty-eight hours. In no case was there the slightest difficulty in distinguishing the human blood from animal blood at the primary experiment, but the greatest care was necessary in the details of the experiments to avoid any contamination. In one experiment a striking result which could not be at first explained was subsequently found to be due to a contamination.

Should this test upon further investigation prove as satisfactory as now seems probable, it will still be most essential in its practical application that the experimenter have experience, not alone with this method, but with the management of injections and serum work generally. Should the test be used in medico-legal cases, I believe that it is most essential that the experimenter's experience in serum and blood work generally be carefully scrutinized before his results are accepted.

With regard to the applicability of this test, Uhlenhuth, Stern, Nuttall, Grünbaum and others have studied the effects of the serum of the blood of various forms of monkeys and apes. Uhlenhuth had positive results with baboon's blood. Stern used three different kinds of monkeys—a species of *Cercopithecus*, *Macacus Cynomolgus* (Java Ape) and the Crown Ape. Nuttall used four species of monkeys—*Cercopithecus Campbelli*, *Cercopithecus Patas*, *Cercopithecus Lalandii* and *Macacus Rhesus*. Grünbaum has tested the gorilla, orang and chimpanzee in particular. Stern found feeble reactions with the three species of monkeys employed. Nuttall found a slight reaction with the blood of the four monkeys tested, and Grünbaum found reactions with the three animals used by him, and also found that human blood was precipitated by rapid serum from animals injected with the blood of the gorilla, orang, chimpanzee.

In a later communication Nuttall reports that in testing 140 specimens of blood none excepting monkey blood gave the reaction with the anti-serum for human blood. He states that all the bloods of the Old World monkeys gave a marked reaction, less powerful, however, than that of human blood. They also reacted to weak anti-serum. On the other hand, the South American monkey gave but a slight reaction with human dilute serum and a weak anti-serum produced no precipitation in the blood of *Myctes Senicu-*

lus. He concludes that, while the tests require further study, the result corresponds with the Darwinian theory of the relationship between man and ape—the relation of the former, according to that theory, being closely to the Old World apes. The anti-serum for dog's blood when tested with 140 bloods reacted only with the blood of the jackal of South Africa. None of the 140 bloods gave a reaction with the anti-serum for horse's blood. No member of the horse family was tested.

In some cases blood serum of rabbits treated with heterologous blood have reacted in a way not specific. Thus Nuttall found the serum from a rabbit treated with ox blood reacted with the blood of the gazelle and axis deer and gave slight cloudiness with the blood of sheep, gnu, squirrel and swan. In no case, however, as far as I have discovered, has the humanized serum of rabbits reacted excepting to the blood of man or species of the monkey family.

With regard to the applicability of this test in medico-legal cases, it may be of interest to report a case studied by Prof. Wood, of Harvard Medical School. The test was applied in a murder case tried in New Hampshire. The blood of a stain on the right elbow of a brown jacket, about one-quarter inch in diameter; another, about one-half inch in diameter on the front of a jacket, were utilized. One-half of the elbow stain was cut out and soaked with distilled water and the other stain was scraped over half its extent, the scrapings being caught in a watch-glass and the powder treated with distilled water. This distilled water solution was placed in a small test-tube and treated with an equal volume of double normal salt solution. Four little spats of blood on the leg of a pair of overalls were treated in the same manner and also a stain of about one-quarter inch in diameter on the other leg. A few threads from two blood stains on a towel were cut out and a solution made as before described. Also some clotted blood found on a stone, the latter being the implement with which the murder was committed. All of these solutions were placed in small test-tubes side by side, and for purposes of comparison several other solutions of dried human blood, of that of a dog, ox, pig and sheep were employed. To each test-tube one, two or three drops of the testing serum were added. A distinct precipitation occurred within one-half hour in the test-tubes containing the blood obtained from both stains on jacket, the legs of overalls, the stain on the towel, the blood on the stone and in the test-tubes containing the human blood. No pre-

cipitation or cloudiness was obtained from the blood of the dog, pig, ox and sheep.

Several other instances of the medico-legal use of this test have been reported unofficially. The official reports will probably be published in the near future. While the reaction is not absolutely a specific one, occurring as has been pointed out in certain other animals, it seems to be reliable in distinguishing human blood from the blood of those domestic or common mammalian animals whose corpuscles most nearly resemble human blood corpuscles. While, therefore, it may not wholly replace studies of the size of corpuscles and differential counts of leucocytes to determine the percentage of different forms of granules, yet, as a method of medico-legal differentiation, it is a powerful adjuvant and is undoubtedly by far the most useful test at the present time. Some experiments in the direction of agglutination of red blood corpuscles by serum of immunized rabbits give promise that in the future this method may supplement the method of precipitation. It is too early, however, to consider this method, which has certainly not as yet reached the dignity of a practical procedure.

*Stated Meeting, December 19, 1902.*

President WISTAR in the Chair.

The list of donations to the Library was laid on the table and thanks were ordered for them.

The President appointed Mr. Henry Pettit to prepare an obituary notice of the late Joseph M. Wilson.

The resignations of Messrs. C. Hanford Henderson and of Samuel N. Rhoads were received and accepted.

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